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A SURVEY OF THE EUROPEAN VALVATIFORM HYDROBIID GENERA, WITH SPECIAL REFERENCE TO *HAUFFENIA* POLLONERA, 1898 (GASTROPODA: HYDROBIIDAE)

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ABSTRACT

All the taxa of genus and species groups introduced for the European valvatiform hydrobiids are analyzed, and if possible revised.

All the type species have been redescribed on the basis of new anatomical studies or data in the literature when spirit specimens were not available. This enabled the following taxa to be recognized as junior synonyms of *Hauffenia* Pollonera, 1898 (type species *Horatia* (*Hauffenia*) *tellinii* Pollonera, 1898): *Erythropomatiana* Radoman, 1978 (type species *Valvata erythropomatia* Hauffen, 1856); *Lobaunia* Haase, 1993 (type species: *Lobaunia danubialis* Haase, 1993); *Neohoratia* Schütt, 1961 (type species *Valvata* (?) *subpiscinalis* Kuščer, 1932); and *Vrania* Radoman, 1978 (type species *Valvata wagneri* Kuščer, 1928).

Of the species currently assigned to *Hauffenia,* only a few from the eastern Alps and Balkans actually belong to it: *H. erythropomatia* (Hauffen, 1856); *H. kerschneri* (Zimmermann, 1930); *H. media* Bole, 1961; *H. subcarinata* Bole & Velkovrh, 1987; *H. subpiscinalis* (Kuščer, 1932); *H. tellinii* (Pollonera, 1898) (with *H. michleri* Kuščer, 1932, as junior synonym); *H. tovunica* Radoman, 1978; *H. wagneri* (Kuščer, 1928); and *H. wienerwaldensis* Haase, 1992. Each is redescribed.

Many "*Hauffenia*" species from the Balkans remain of uncertain generic status due to the absence, or incompleteness of anatomical data. However, *Horatia* (*Hauffenia*) *raehlei* Schütt, 1980, is placed in the genus *Fissuria* Boeters, 1981, on the basis of its anatomy.

After anatomical study, most of the French "*Hauffenia*" have been assigned to *Islamia* Radoman, 1973a, and tentatively to the following species: *I. minuta* (Draparnaud, 1805), *I. globulina* (Paladilhe, 1866), *I. spirata* (Bernasconi, 1985), and *I. consolationis* (Bernasconi, 1985). Anatomical study of the French "*Horatia*" *exilis* (Paladilhe, 1867) supports its allocation to a new genus: ***Heraultia,*** n. gen.

The Spanish species currently assigned to "*Horatia*" or "*Neohoratia*" do not belong to these genera. Some of them, namely "*N.*" *ateni* (Boeters, 1969), "*N.*" *globulus globulus* (Bofill, 1909), and "*N.*" *g. lagari* (Altimira, 1960), belong to *Islamia.*

Diagnoses and keys are provided for the European valvatiform hydrobiid genera and for the species of *Hauffenia,* together with tables summarising their taxonomic status and distribution.

Key words: Gastropoda, Caenogastropoda, valvatiform Hydrobiidae, taxonomy, systematics, geographical distribution, Europe.

INTRODUCTION

The European fauna is particularly rich in valvatiform stygobiont hydrobiids (Radoman, 1983; Bole & Velkovrh, 1986). The first species discovered were assigned to the heterobranch valvatid genus *Valvata* Müller, 1774, until the first hydrobiid genera were described. Since the 1950s, a plethora of new genera and new species have been introduced. This produced a puzzling taxonomic picture, with genera established on shell and/or few anatomical characters, frequent changes of rank of many supraspecific taxa, and species (including extra-European; see Bole & Velkovrh, 1986) assigned to genera on the basis of non-diagnostic characters. In an attempt to reduce this taxonomic chaos, we set out to revise all the taxa related to one of the oldest established genera, *Hauffenia* Pollonera, 1898.

Hauffenia was introduced by Pollonera (1898) as a subgenus of *Horatia* Bourguignat, 1887, for two new hydrobiids, collected by A. Tellini in the debris of the upper course of the Natisone River, Friuli, northeastern Italy: *Horatia tellinii* and *H. valvataeformis.*

Kuščer (1932, 1933a, b) ranked *Hauffenia*

as a distinct genus, but this was not substantiated until Bole (1970) studied the anatomy of *H. tellinii* and found that its genitalia were different from that described by Radoman (1966) for the type species of *Horatia*. Bole (1970) listed three diagnostic characters of *Hauffenia:* (1) female genitalia with a small bursa copulatrix having short duct arising from the oviduct near where it enters the albumen gland (pallial oviduct), and a very small seminal receptacle arising from the renal oviduct where the oviduct loop ends; (2) male genitalia with a wide and flat penis; and (3) operculum with peg-like structure on its inner face.

Boeters (1974) split *Hauffenia* into two subgenera, *Hauffenia* (*s. s.*) and *Neohoratia*, the latter introduced by Schütt (1961a) as a subgenus of *Horatia* for *Valvata subpiscinalis* Kuščer, 1932. Boeters (1974) regarded *Neohoratia* as a subgenus of *Hauffenia* because *H. subpiscinalis* shares the genital characters of the species of *Hauffenia* (*s. s.*), but it has no peg-like structure on the inner face of the operculum.

Oddly, Radoman (1978, 1983) overlooked *Neohoratia* but divided *Hauffenia* into two subgenera: *Hauffenia* (*s. s.*) and *Vrania* Radoman, 1978 (type species: *Valvata wagneri* Kuščer, 1928), the latter characterized only by an operculum with a thin edge and a small outgrowth on its inner face. Radoman (1978, 1983) also introduced a number of new genera from the Balkans, one of these, *Erythropomatiana* Radoman, 1978 (type species: *Valvata erythropomatia* Hauffen, 1856), had an organization of the female genitalia similar to that of *Hauffenia*.

Subsequently, Bole & Velkovrh (1986) and Boeters (1988, 1998) ranked *Neohoratia* as a distinct genus. Boeters (1988, 1998) probably based this assumption on the fact that three Iberian species and one French species, supposed by him to be congeneric with *N. subpiscinalis*, had differently organized female genitalia: the sac-like structures arising from the renal oviduct are two seminal receptacles and not a bursa copulatrix and a seminal receptacle, as in *Hauffenia*. Recently, Bole (1993) re-examined the Slovenian taxa of this group, confirming *Hauffenia, Erythropomatiana* and *Neohoratia* as distinct genera, although they were characterized by rather insignificant anatomical characters. On the other hand, he treated *Vrania* as a junior synonym of *Hauffenia,* as proposed independently by Haase (1993).

In this paper, we redescribe *Hauffenia* and define its relationships with nominal genera claimed to have similar anatomical organization (e.g., *Erythropomatiana, Neohoratia*, and *Vrania*). To do this, we first consider all the genera of the European valvatiform hydrobiids and redescribe their type species on the basis of literature and our own data. We also revise all the specific taxa assigned to these genera, claryifing which actually belong to *Hauffenia* and which belong to other genera. Each *Hauffenia* species is redescribed in the second section of the paper and a few misidentified *Hauffenia* species are redescribed and discussed.

MATERIAL AND METHODS

Shells and live specimens were collected by sorting variable amounts of sediment from caves and springs. Unrelaxed material preserved in 75% ethanol was studied by light microscopy (Wild M5A). Bodies were isolated after crushing the shells and were dissected using very fine, pointed watchmaker's forceps. Images of the body and isolated parts of the genitalia were drawn using a Wild camera lucida. Radulae were obtained by dissecting out buccal bulbs and soaking them in KOH solution to remove soft tissue. They were washed in distilled water, mounted on copper blocks with electronconductive glue, sputter-coated with gold, and photographed using a Philips 505 SEM. Shells and shell fragments were photographed under light and scanning electron microscopes.

The anatomical parts are disposed as in life position. So when the penis is described, terms such as left, right, ventral and dorsal correspond to the left, right, ventral and dorsal sides of the snail in life position. When a structure belonging to an organ is described, its position is indicated in relation to the proximal origin of the organ (e.g., "at about 2/3 of penis length" means about 2/3 of the distance from the base to the apex of penis). The terms used in the description are those recently proposed by Hershler & Ponder (1998), except for the following (parentheses-terminology of Hershler & Ponder, 1998): last whorl (body whorl); protoconch malleated (pitted or wrinkled); right (outer) or left (inner) side of penis; seminal groove (ventral channel); lateral wings of central tooth (lateral margins); lamellae (filaments). We prefer these terms because they are in current use by European

authors or describe the aspect or function of the structure more exactly.

In the description of the taxa, any reference to a structure will be omitted when its presence/absence has been impossible to ascertain in an unequivocal manner (e.g., the hypobranchial gland) or when data in the literature is insufficient to allow their exact definition (e.g., the route of the penial duct).

For identification of the different sac-like structures arising from the distal renal oviduct we adopted the following criteria, in the absence of histological evidence:

- the proximal seminal receptacle (PSR; second or RS2, according to Radoman, 1973b, 1983) leaves the oviduct far from the bursa and level with the end of the oviduct loop;
- the distal seminal receptacle (DSR; first or RS1, according to Radoman, 1973b, 1983) arises very close to the point where the oviduct enters the albumen gland (pallial oviduct) but proximally with respect to the bursa copulatrix; it is obviously easy to identify when the bursa is present; when the bursa is absent, it can be identified by the fact it arises further from where the oviduct enters the albumen gland than any bursa, and consequently lies in a position corresponding to that of the DSR in species that also have a bursa;
- the bursa copulatrix (BC) arises close to the point where the oviduct enters the albumen gland (pallial oviduct).

When histological evidence exists, the bursa copulatrix (gametolytic gland) is a structure that does not contain spermatozoa or contains few, non-oriented and partially digested spermatozoa (its contents are centrally located and never refringent), whereas the seminal receptacle/s is/are the structure/s that contains/contain spermatozoa oriented with their heads anchored to the cells of the wall (Thompson & Bebbington, 1969; Giusti & Selmi, 1985).

For histological study, the penis was fixed in 75% ethanol, dehydrated, diaphanized with xylol, and mounted on microscope slides. The female genitalia (renal and pallial oviduct) were fixed in 75% ethanol, dehydrated, embedded in paraffin and cut serially; sections mounted on microscope slides were stained with haematoxylin-eosin.

The material examined is listed as follows: locality name (municipality, district and/or country), UTM references, collector(s) and date (number of male and female specimens, shells, non-investigated specimens).

Parsimony analysis was performed using a test version of PAUP (Version 4.0.b2 for Macintosh; Swofford, 1997). Tree search was performed using the heuristic search and the "collapse branches if minimum length is zero" options. The characters used for cladistic analysis were chosen on the list of Hershler & Ponder (1998). Only the type species of each genus was considered or, alternatively, that regarded to be the most closely related species, if the anatomy of the type species is not known.

Much of the literature on the valvatiform hydrobiids published after the fifties by S. Hadžišče and P. Radoman has questionable publication dates and conditions regarding the availability of the names. The main problem concerns the date of publication of two papers (one by Hadžišče and the other by Radoman) on the hydrobiids of Lake Ohrid. Radoman (1963a: 69; b: 85–86) claimed that Hadžišče paper was published in 1959 and his paper in 1957: "Hadžišče's paper, although antedated to August, 1956, was actually issued only in April, 1959 (date taken from the inventory of the Hydrobiological Institute at Ohrid), while my paper was issued in October, 1957 (date taken from the inventory of the Publishing Department of Kolorac National University . . . in Beograd" (Radoman, 1963b: 86). Unfortunately, Radoman (1963a, b, 1973a, 1983) left room for confusion by continuing to cite the two papers with the putative year of publication (1956) and not the true year of publication (1957 for his paper, 1959 for Hadžišče's paper). This caused misinterpretation by subsequent authors dealing with the taxa established in these papers (Bole & Velkovrh, 1986; Jovanović, 1991; Kabat & Hershler, 1993; Dhora & Welter-Schultes, 1996).

We accepted 1957 as the date of publication of Radoman's paper and 1959 as the date of publication of Hadžišče's paper. In the case of species described by both authors, Radoman's names therefore have priority over those of Hadžišče. Consequently *Ohrigocea* (*Karevia*) *prlitchevi* Hadžišče, 1959, is a junior synonym of *Pseudamnicola ornata* Radoman, 1957, and *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici* Hadžišče, 1959, is a junior synonym of *Pseudamnicola depressa* Radoman, 1957.

Other problems were caused by the fact that Radoman (1973a) established many nominal genera without a description or definition but only by combining them with available or new included nominal species. Some of these nominal genera were available at the

first introduction (*Bracenica, Daphniola, Islamia* and *Strugia*), others were only made available subsequently (*Dolapia, Prespolitorea* and *Zaumia*), and others have never been made available (*Naumia, Ohridosturanya* and *Rotondia*).

Key to acronyms in figures: AG, albumen gland; BC, bursa copulatrix; C, ctenidium; CG, capsule gland; CS, cuticularized structure (stylet); DSR, distal (first or RS1) seminal receptacle; FP, fecal pellets; GPD, gonopericardial duct; HG, hypobranchial gland; I, intestine; LO, loop of the oviduct; MP, muscular pleat; OC, opercular crest; OE, oesophagus; OP, opercular peg; OS, osphradium; OT, opercular thickening; P, penis; PD, penial duct; PG, prostate gland; PGL, penial glandular lobe; PL, penial lobe; PSR, proximal (second or RS2) seminal receptacle; PW, posterior wall of pallial cavity; R, rectum; RC, mass of refringent cells; S, stomach; SG, seminal groove; VD, vas deferens; VE, vas efferens (seminal vesicle).

A SURVEY OF THE EUROPEAN VALVATIFORM HYDROBIID GENERA

Arganiella Giusti & Pezzoli, 1980

Arganiella Giusti & Pezzoli, 1980: 45.

Type Species: *Arganiella pescei* Giusti & Pezzoli, 1980, by monotypy.

Arganiella pescei Giusti & Pezzoli, 1980

Arganiella pescei Giusti & Pezzoli, 1980: 45–46, fig. 19A–C.

Type Locality: "reticoli di falda delle Marche, dell'Abruzzo e del Lazio (in questa regione limitatamente alla provincia di Rieti)", Italy. Restricted by Giusti & Pezzoli (1981: 213) to: "Pozzo 163, lungo la SS 150, 32 m slm, 42°30′13″N, 01°27′55″E (versante orientale dell'Appennino centrale, in provincia dell'Aquila, Abruzzo [Well no. 163, along state road no. 150, Km 9.8, altitude 32 m, 42°30′13″N, 01°27′55″E, western side of central Apennines, province of L'Aquila, Abruzzo, Italy]" (actually, the restricted type locality is not in L'Aquila, but in Teramo).

Type Material: holotype (shell) is in the Giusti collection, Siena, Italy; three paratypes (SMF 254290, shells) are at the Senckenberg-Museum, Frankfurt am Main, Germany, and others (shells and preserved specimens) in the Giusti and Pezzoli collections, Milan, Italy (Giusti & Pezzoli, 1981).

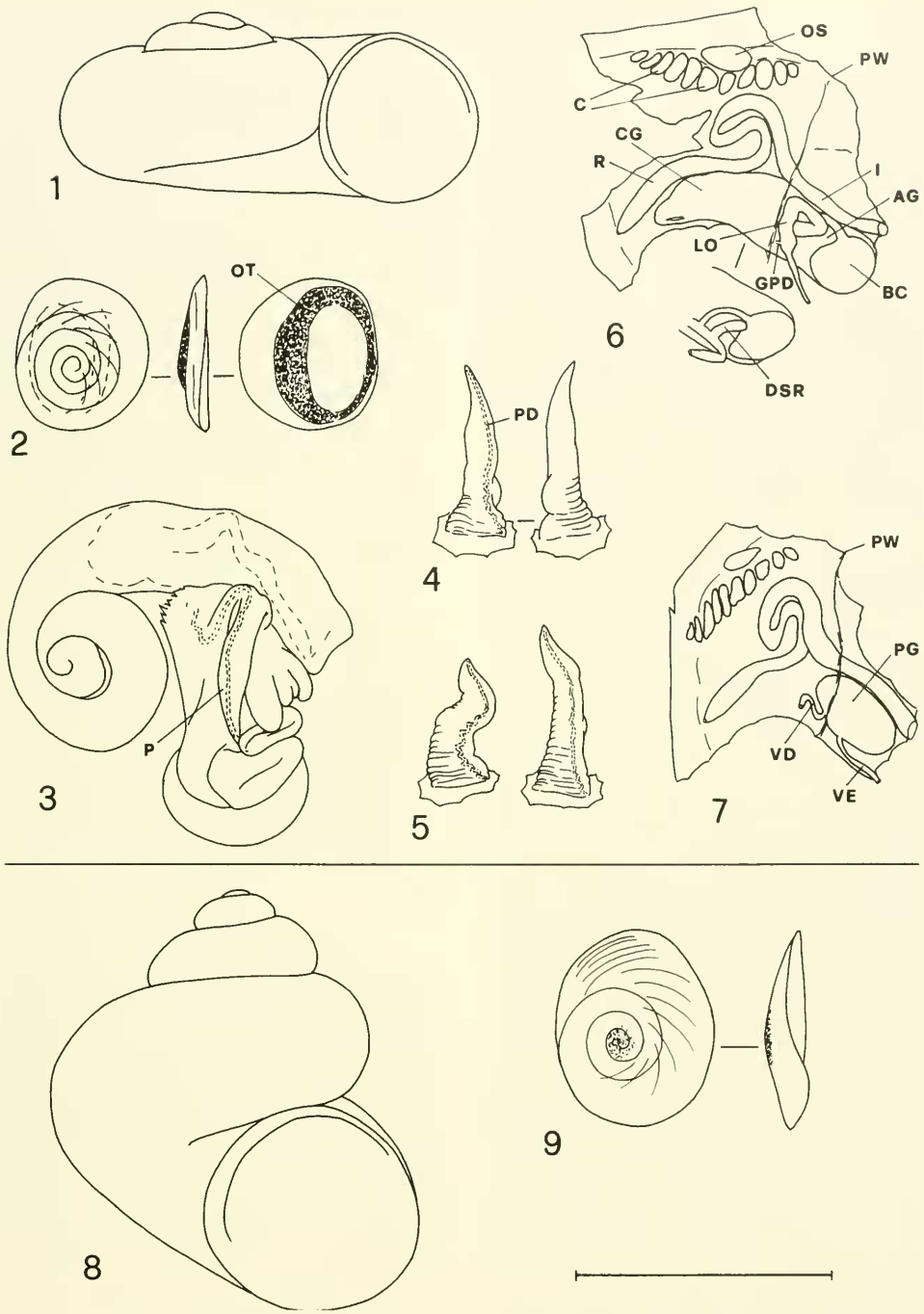
Material Examined

- Well no. P/163 along the state road 150, km 9.8, Teramo, Abruzzo, Italy, 33T VH 12, R. Argano & G. L. Pesce leg. 3.5.1975 (2 males, 1 female, some shells) (Pesce & Silverii, 1976).
- Well no. P/161 near S. Petronilla, Roseto, Teramo, Abruzzo, Italy, 33T VH 12, R. Argano & G. L. Pesce leg. 3.5.1975 (3 males, 3 females, many specimens) (Pesce & Silverii, 1976).
- Well no. P/42, state road 17, Contrada Buccella, L'Aquila, Abruzzo, Italy, 33T UG 69, G. L. Pesce leg. 16.12.1972 (1 male, 1 specimen) (Argano et al., 1975).
- Well no. P/37, state road 17, turn-off to Sassa, before Raio Stream, L'Aquila, Abruzzo, Italy, 33T UG 59, G. L. Pesce leg. 9. 1976 (3 males, 5 females, many specimens) (Argano et al., 1975).
- S. Susanna springs, Rivodutri, Rieti, Latium, Italy, 33T UH 2307, M. Bodon leg. 12.4.1993 (5 shells), M. Bodon & G. Manganelli leg. 29.6.1995 (2 males, 1 female, 7 shells).
- Well no. R/23, Via Salaria, km 88.8, Rieti, Latium, Italy, 33T UG 29, G. L. Pesce leg. 13.6.1973 (1 female) (Pesce & Fusacchia, 1975).
- Well no. R/28, Madonnella, Via Cicolana, Km 5.6, Rieti, Latium, Italy, 33T UG 29, G. L. Pesce leg. 13.6.1973 (1 male, 1 specimen) (Pesce & Fusacchia, 1975).

For other localities where only shells have been found see Giusti & Pezzoli (1981).

Description

Shell very small, valvatiform to planispiral, thin, pale whitish, glassy, transparent when fresh; surface of protoconch malleated; spire from rather raised to almost flat, consisting of 2.75-3 rather rapidly growing convex whorls; last whorl large, dilated, more or less descending near aperture; umbilicus wide; aperture prosocline, roundish, sometimes pyriform; peristome complete, slightly thickened, slightly reflected only at lower and columellar margin (Figs. 1, 10; Giusti & Pezzoli, 1980:



FIGS. 1–9. Shell, operculum and anatomical details of *Arganiella pescei* Giusti & Pezzoli, 1980, from well no. P/37, state road 17, cross-roads for Sassa, before the Raio stream, L'Aquila, Abruzzo, Italy, G. L. Pesce leg. 9.1976 (Figs. 1–7) and shell and operculum of *Daphniola exigua* (Schmidt, 1856) from the spring Daphne in the Tembe valley, Thessalia, Greece, 7.1980, *ex* W. J. M. Maassen collection (Figs. 8–9). Figs. 1, 8: shell; Figs. 2, 9: outer face (left), profile (centre in Fig. 2; right in Fig. 9) and inner face (right in Fig. 2) of operculum; Fig. 3: body of a male with pallial cavity open to show head and penis; Figs. 4, 5: penis of three males, dorsal side (left in Figs. 4, 5) and ventral side (right in Fig. 4); Fig. 6: renal and pallial oviduct, intestine and pallial organs of a female; Fig. 7: male genitalia (penis and testis excluded), intestine and pallial organs. Scale bar = 1 mm.

45, fig. 19A; 1981: 208–209, figs. 3, 7). Dimensions: height = 0.85–1.05 mm; diameter = 1.65–2.00 mm.

Operculum thin, yellowish white or yellowish orange, paucispiral, slightly thickened and often with a circular thickening at centre of inner face (Fig. 2; Giusti & Pezzoli, 1980: 45; 1981: 208, 213, fig. 2E).

Body unpigmented; eye spots absent (Fig. 3; Giusti & Pezzoli, 1980: 45, fig. 19B; 1981: 208, 213, figs. 1F, 2A).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis from short to elongated, flat, with sides corrugated, slightly dilated then tapering near apex, usually ending in very pointed tip; penis without lobes, but sometimes with a crest or a small swelling on ventral side near base; penial duct zig-zagging through right portion of penis, opening at penis tip (Figs. 4, 5, 7; Giusti & Pezzoli, 1980: 45, fig. 19; 1981: 208–209, fig. 1F–O).

Female genitalia with distal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle rather developed, arising from oviduct close to point of origin of duct of bursa copulatrix; bursa copulatrix large, sac-like or kidney-shaped, with rather long duct entering on anterior side; seminal groove running along ventral side of capsule gland (Fig. 6; Giusti & Pezzoli, 1980: 45, fig. 19C; 1981: 208–209, fig. 1A–C).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its cutting edge V-like, with long robust central denticle and 5-6 smaller denticles on both sides in decreasing order of size; two basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth apically enlarged, their cutting edge with 9–11 denticles, central of which longer, larger; first marginal teeth with long lateral wing and elongated apex, its cutting edge with long row of 20–22 small denticles; second marginal teeth with long, slender lateral wing and roundish, spoon-like apex with cutting edge carrying rather long row of 18–20 very small denticles (Giusti & Pezzoli, 1980: 45; 1981: 208–229, 212, figs. 5A–D).

Stomach without posterior caecum; intestine with well-developed, U- or S-like bend on pallial wall (Figs. 6, 7; Giusti & Pezzoli, 1980: fig. 19C; 1981: 213, figs. 1A, B, 2A–D, F).

Osphradium variable in size, oval or kidney-shaped; ctenidium consisting of 9–18 lamellae (Figs. 6, 7; Giusti & Pezzoli, 1980: 45, fig. 19C; 1981: 208, 213, figs. 1A–B, 2A, F).

Nervous system unknown.

Taxonomy

The genus *Arganiella* is characterized by: shell very small, valvatiform to planispiral; operculum without peg; penis without lobes; female genitalia with distal seminal receptacle and large, sac-like or kidney-shaped bursa copulatrix with anterior duct; central tooth with two pairs of basal cusps. It includes only the type species, which is endemic to the central Apennine, Italy. Another species, the French *Valvata exilis* Paladilhe, 1867, was erroneously assigned to this genus by Bouchet (1990) (see "Description of a new valvatiform genus from France").

Bracenica Radoman, 1973a

Bracenica Radoman, 1973a: 7, 20.
Type Species: *Bracenica spiridoni* Radoman, 1973a, by monotypy.

Bracenica spiridoni Radoman, 1973a

Bracenica spiridoni Radoman, 1973a: 7, 20.
Type Locality: "Špirov izvor, Podmeret, near Braćeni, not far from Virpazar, Crna Gora", Montenegro.
Type Material: lectotype (BEO 116, shell) at the Prirodnjacki Muzej u Beograd together with a paralectotype (BEO 117, shell) (Jovanović, 1991).

Description

Shell very small, valvatiform-planispiral; surface of protoconch unknown; spire depressed, consisting of 2.75–3.25 rather rapidly growing convex whorls, first whorls slightly raised, last whorl large; umbilicus very wide, deep; aperture roundish to oval; peristome complete, thin, slightly reflected only at its lower and columellar margin (Radoman, 1973a: 20; Radoman, 1983: 65, pl. 4, fig. 58; Jovanović, 1991: pl. 4, fig. 26). Dimensions: height = 0.92–1.18 mm; diameter = 1.64–2.02 mm (Radoman, 1983: table 4).

Operculum thin, whitish with yellow central part and peg on inner face (Radoman, 1983: 66).

Body unpigmented; eye spots absent (Radoman, 1983: 66).

Male genitalia with penis elongated and pointed, with one, evident, knob-like lobe on left side about half way along penis (Radoman, 1973a: 20; 1983: 66, fig. 29).

Female genitalia with two seminal recepta-

cles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle very small; distal seminal receptacle very large, club-shaped; bursa copulatrix large, pyriform, with long slender duct that enters bursa on anterior side (Radoman, 1973a: 6, 20; 1983: 40, 66, fig. 29).

Radula with central tooth with one pair of basal cusps; other details unknown (Radoman, 1973a: 6; 1983:40).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1983: 66).

Taxonomy

Radoman (1973a: 7, 20) established *Bracenica* without a description or definition but only giving a combined description of it and a single included new nominal species. This makes *Bracenica* available (ICZN, 1999: Art. 13.4).

Bracenica is a little known genus characterized by: shell very small, valvatiform-planispiral; operculum with peg; penis with one simple lobe; female genitalia with two seminal receptacles, distal larger than proximal, and large, pyriform bursa copulatrix with anterior duct. It contains only the type species from Montenegro.

Dabriana Radoman, 1974

Dabriana Radoman, 1974: 81.

Type Species: *Dabriana bosniaca* Radoman, 1974, by original designation.

Dabriana bosniaca Radoman, 1974

Dabriana bosniaca Radoman, 1974: 81–84, figs. 1–3A–D.

Type Locality: "Dabarska [Dabarška] pećina, neben dem Ursprung des Flüsschen Dabar, etwa 6 Km südlich der Stadt Sanski most, Bosnien". According to Radoman (1983: 168), the type locality is "Dabarska [Dabarška] pečina (cave), by the source of the Dabar river, about 6 km south of the Sanski Most town".

Type Material: the holotype and six paratypes (SMF 232168) are at the Senckenberg-Museum, Frankfurt am Main, Germany (Jovanović, 1991).

Description

Shell very small, valvatiform, whitish, transparent when fresh; microsculpture of protoconch unknown, surface of teleoconch with fine radial striations; spire moderately raised, consisting of 3.25–3.5 rapidly growing convex whorls; last whorl dilated, slightly descending near aperture; umbilicus moderately wide; aperture large, prosocline, roundish; peristome complete, slightly reflected only at columellar margin (Radoman, 1974: 81, fig. 1; 1983: 167–168, pl. 11, figs. 201, 202; Jovanović, 1991: pl. 10, fig. 6). Dimensions: height = 1.85–2.18 mm; diameter = 2.06–2.49 mm (Radoman, 1983: 208, table 9).

Operculum probably without outgrowth, though not specified (Radoman, 1974: fig. 3A; 1983: fig. 102A).

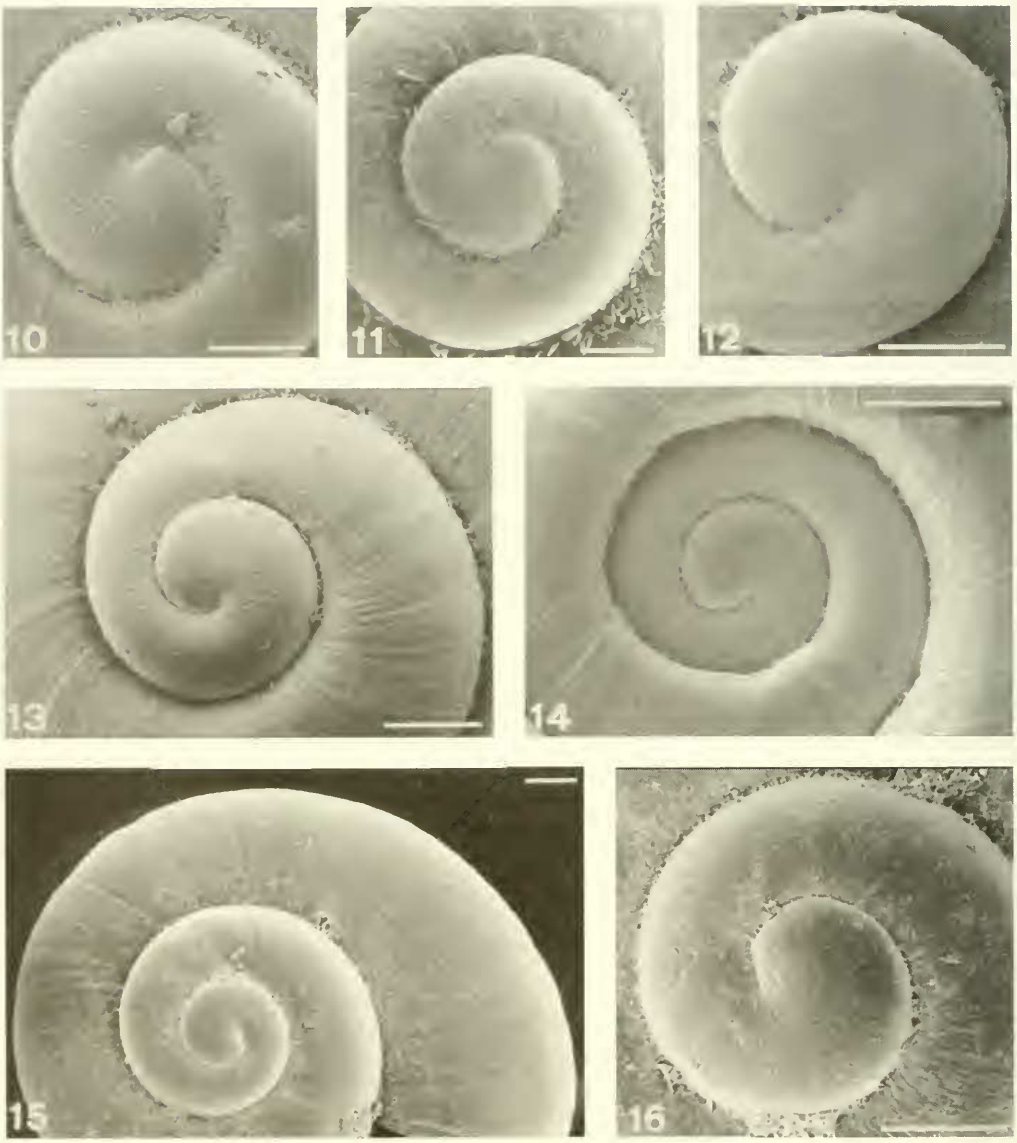
Body unpigmented; eye spots absent; caudal tentacle at posterior apex of foot (Radoman, 1974: 81, figs. 1, 3A; 1983: 168, fig. 102A, pl. 11, fig. 202).

Male genitalia with penis conical elongated, without lobes; penial apex slender, pointed (Radoman, 1974: 82, fig. 3A, B; 1983: 168, fig. 102A, B).

Female genitalia with a seminal receptacle (probably distal) and a bursa copulatrix; seminal receptacle very large, ovoid, protruding posteriorly, with evident duct inserted halfway between end of oviduct loop and bursa copulatrix duct; bursa copulatrix very small, elliptical, with short duct entering bursa on anterior side; capsule gland divided in two parts, the anterior of which narrow; seminal groove running all along ventral side of capsule gland (Radoman, 1974: 81–82, fig. 3C, D; 1983: 167–168, fig. 102 C, D).

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin with robust central denticle and about 6 smaller denticles on both sides in decreasing order of size; no basal cusp at point where lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with about 6 large denticles, central of which larger; first marginal teeth rake-shaped, with a long lateral wing and elongated cutting edge with a long row of about 14 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, cutting edge of which carrying rather long row of small denticles (Radoman, 1974: 81, fig. 2; 1983: fig. 101).

Stomach without posterior caecum; intes-



FIGS. 10–16. Microsculpture of protoconchs. Fig. 10: *Arganiella pescei* Giusti & Pezzoli, 1980, from well no. P/37, state road 17, cross-roads for Sassa, before the Raio stream, L'Aquila, Abruzzo, Italy, G. L. Pesce leg. 9.1976; Fig. 11: *Daphniola exigua* (Schmidt, 1856) from the spring Daphne in the Tembe valley, Thessalia, Greece, 7.1980, *ex* W. J. M. Maassen collection; Fig. 12: *Hauffenia erythropomatia* (Hauffen, 1856) from "Babja Luknja" cave, S. 35, Goričane, Medvode, Slovenia, M. Bodon leg. 16.6.1985; Fig. 13: *Fissuria boui* Boeters, 1981, from the spring La Foux, Draguignan, Var, France, M. Bodon leg. 7.1.1990; Fig. 14: *Hadziella ephippiostoma* Kuščer, 1932, from the springs Močilnik, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985; Figs. 15, 16: *Hauffenia tellinii* (Pollonera, 1898) from the spring between Spagnut and Biacis, upper Natisone valley, Pulfero, Udine, Friuli-Venetia Julia, Italy, M. Bodon leg. 9.6.1985. Scale bar = 100 μm.

tine unknown (Radoman, 1974: 82; 1983: 166).

Osphradium elliptical; ctenidium absent (Radoman, 1974: 81; 1983: 168).

Nervous system with very long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1974: 81–82; 1983: 166).

Taxonomy

Dabriana is a little-known genus characterized by: shell very small, valvatiform; operculum without peg; foot with caudal tentacle; penis without lobes; female genitalia with large, probably distal, seminal receptacle and very small, elliptical bursa copulatrix with anterior duct; central tooth of radula without basal cusps. It contains only the type species from Bosnia-Herzegovina.

Radoman (1983) dubiously places this genus in the Lithoglyphulidae, but Bole & Velkovrh (1986) and Kabat & Hershler (1993) assigned it to the Hydrobiidae. It shares some characters (central tooth of the radula without basal cusps; foot with caudal tentacle) with some marine rissooids.

Dalmatella Velkovrh, 1970

Dalmatella Velkovrh, 1970: 97, 103.

Type Species: *Dalmatella sketi* Velkovrh, 1970, by original designation.

Dalmatella sketi Velkovrh, 1970

Dalmatella sketi Velkovrh, 1970: 97–98, 103, fig. 1A–D.

Type Locality: "izvir pri odtoku Krke izpod elektrarne pod Skradinskim Bukom (Šibenik, Dalmacija)", Croatia. It corresponds to the "spring under power stations near Skradinski Buk on the river Krka" (Bole & Velkovrh, 1986: 190).

Type Material: holotype (9075/1) in the Velkovrh collection, Ljubljana, Slovenia, together with three paratypes (9075/2–4) (Velkovrh, 1970).

Description

Shell very small, valvatiform, keeled, convex above, rather flat below, transparent when fresh; microsculpture of protoconch unknown; spire rather raised, consisting of 3.66 rather rapidly growing whorls; last whorl large, trapezoidal in outline, with marked, rather sharp peripheral keel at base, slightly dilated, descending near aperture; umbilicus wide; aperture prosocline, oval to roundish, with sort of beak at keel; peristome complete, sinuous, not thickened, slightly reflected only at lower and columellar margin (Velkovrh, 1970: 97–98, 103, fig. 1A–D; Bole & Velkovrh, 1986, fig. 15). Dimensions: height = approximately 1.6 mm; diameter = approximately 2.2 mm (Velkovrh, 1970: 98).

Operculum and anatomy unknown.

Taxonomy

A relatively unknown genus, including only the type species and another undescribed entity (Bole & Velkovrh, 1986), both from Croatia. *Dalmatella* is listed as a distinct taxon, but due to lack of anatomical data, its validity is doubtful.

Daphniola Radoman, 1973a

Daphniola Radoman, 1973a: 8.

Type Species: *Daphniola graeca* Radoman, 1973a, by monotypy. *Daphniola graeca* is a junior synonym of *Valvata exigua* Schmidt, 1856, according to Schütt (1980), and a junior synonym of *Valvata (Cincinna) hellenica* Westerlund, 1898, according to Reischütz & Sattmann (1993).

Daphniola exigua (Schmidt, 1856)

Valvata exigua Schmidt, 1856: 160.

Type Locality: "Griechenland". Following the designation of the neotype by Schütt (1980), the type locality becomes "Thessalien: mehrere kleine Quellen im Tempetal in der Nähe der Bahnstation Agia Paraskeui".

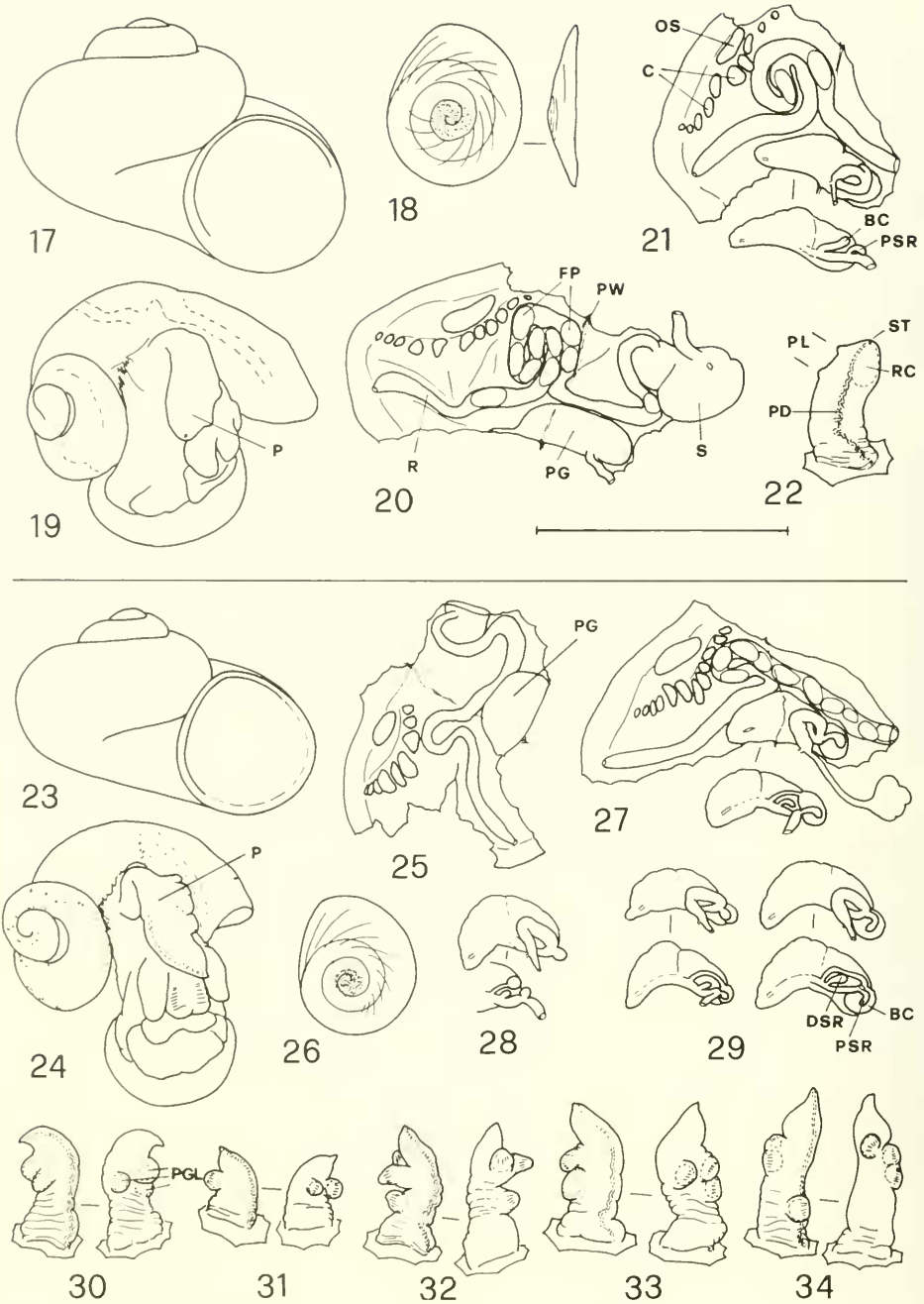
Type Material: neotype (SMF 262352, shell) in the Senckenberg-Museum, Frankfurt am Main, Germany (Schütt, 1980).

Valvata (Cincinna) hellenica Westerlund, 1898: 179.

Type Locality: "Griechenland. Vyteria in Arkadien".

Type Material: lectotype (4667a, shell) in the Naturhistoriska Museet Göteborg, Göteborg, Sweden, together with two paralectotypes (4667b, shells) (Reischütz & Sattmann, 1993).

Daphniola graeca Radoman, 1973a: 8, 22.



FIGS. 17–34. Shell, operculum and anatomical details of *Hauffenia erythropomatia* (Hauffen, 1856) from the spring below "Babja Luknja" cave, Goričane, Medvode, Slovenia, M. Bodon leg. 16.6.1985 (Figs. 17–22) and of *Fissuria boui* Boeters, 1981, from Fontaine de Vaucluse, Vaucluse, France, M. Bodon leg. 1.12.1984 (Figs. 23–26, 28, 33), Source du Vivier, N.D. de Vaucluse, Auribeau-sur-Siagne, Alpes Maritimes, France, M. Bodon leg. 1.1.1991 (Figs. 27, 32), the spring La Foux, Draguignan, Var, France, M. Bodon leg. 7.1.1990 (Figs. 29, 30), the spring La Fouan, Châteauneuf Grasse, Alpes Maritimes, France, M. Bodon, E. Bo & M. Sosso leg. 11.2.1994 (Fig. 31), the spring at the Gorges Mal Infernet, Agay, Var, France, M. Bodon leg. 31.12.1990 (Fig. 34). Figs. 17, 23: shell; Figs. 18, 26: outer face (left in Figs. 18, 25) and profile (right in Fig. 18) of operculum; Figs. 19, 24: body of a male with pallial cavity open to show head and penis; Figs. 20, 25: prostate gland, stomach (excluded in Fig. 25), intestine and pallial organs of a male; Figs. 21, 27: gonadal (excluded in Fig. 21), renal and pallial oviduct, intestine and pallial organs of a female; Fig. 22: penis; Figs. 28, 29: renal and pallial oviduct in three females; Figs. 30–34: penis of four males, dorsal side (left) and ventral side (right). Scale bar = 1 mm.

Type Locality: "spring Daphne, about 30 km north of Larissa, Greece".

Type Material: lectotype (BEO 177, shell) in the Prirodnjacki Muzej u Beograd, together with a paralectotype (BEO 178, shell) (Jovanović, 1991).

Material Examined

–Daphne spring in Tembe valley, Thessalia, Greece, 7. 1980, *ex* W. J. M. Maassen collection (5 shells with dried soft parts).

Description

Shell very small, valvatiform-globose conical; surface of protoconch malleated; spire well raised, consisting of 3–3.5 rather rapidly growing convex whorls; umbilicus small; aperture roundish to oval; peristome complete, its external margin thin, its columellar margin thickened, reflected (Figs. 8, 11; Schütt, 1962: 164, fig. 5, as *Horatia* (*Horatia*) *exigua;* Schütt, 1980: 139–140, pl. 10a, fig. 41, as *Horatia* (*Daphniola*) *exigua;* Radoman, 1973a: 22, as *Daphniola graeca;* Radoman, 1983: 84–85, pl. 5, fig. 87, as *Daphniola graeca;* Jovanović, 1991: pl. 6, fig. 44, as *Daphniola graeca;* Reischütz & Sattmann, 1993, pl. 8a, as *Daphniola hellenica*). Dimensions: height = 1.22–1.52 mm; diameter = 1.30–1.40 mm (according to Schütt, 1962: 164, as *Horatia* (*Horatia*) *exigua*); height = 1.1–1.3 mm; diameter = 1.0–1.2 mm (according to Radoman, 1983: 203, table 5, as *Daphniola graeca*).

Operculum thin, yellowish brown, paucispiral, slightly thickened at centre, without outgrowth on inner face (Fig. 9; Schütt, 1962: 163, as *Horatia* (*Horatia*) *exigua;* Radoman, 1973a: 22, as *Daphniola graeca;* Schütt, 1980: 140, as *Horatia* (*Daphniola*) *exigua*).

Body pigmented; eye spots present (Schütt, 1962: 163, as *Horatia* (*Horatia*) *exigua*).

Male genitalia with penis elongated and pointed, with slender lobe on left side at about half penis length (Radoman, 1973a: 22, as *Daphniola graeca;* Schütt, 1980: 140, as *Horatia (Daphniola) exigua;* Radoman, 1983: 83–84, fig. 45, as *Daphniola graeca*).

Female genitalia with two seminal receptacles and a bursa copulatrix (according to Radoman, 1973a, 1983; only one seminal receptacle and bursa copulatrix, according to Schütt, 1980) arising from distal renal oviduct; proximal seminal receptacle markedly larger than distal; bursa copulatrix very large, oval, with long slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1973a: 6, 22, as *Daphniola graeca;* Schütt, 1980: 140, as *Horatia (Daphniola) exigua;* Radoman, 1983: 40, 83, fig. 45, as *Daphniola graeca*).

Radula with central tooth with one pair of basal cusps; other details unknown (Schütt, 1980: 140, as *Horatia (Daphniola) exigua;* Radoman, 1983: 40, as *Daphniola graeca*).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6, as *Daphniola graeca;* Radoman, 1983: 40, as *Daphniola graeca*).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and somewhat shorter pleuro-suboesophageal connectives (Radoman, 1983: 83, fig. 45, as *Daphniola graeca*).

Taxonomy

Radoman (1973a: 8, 22) established *Daphniola* without a description or definition but gave a combined description of it and a single included new nominal species which makes this nominal genus available (ICZN, 1999: Art. 13.4). Thus, *Daphniola* Schütt, 1980 (type species: *Valvata exigua* Schmidt, 1856), is a junior homonym and a junior synonym of *Daphniola* Radoman, 1973a.

Daphniola is here considered a distinct genus. However, some of its anatomical details are unknown and its relationships to other Balkan genera (*Horatia* Bourguignat, 1887, in particular), require further study. *Daphniola* is characterized by: shell very small, valvatiform; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal larger than distal, and very large, oval bursa copulatrix with anterior duct.

According to Schütt (1980), *Daphniola graeca* Radoman, 1973a (p. 22) (type locality: "spring Daphne, about 30 km north of Larissa, Greece") is a junior synonym of *Valvata exigua* Schmidt, 1856. Reischütz & Sattmann (1993) claimed that the identity of the last nominal taxon was uncertain and proposed to use, for this species, *Valvata (Cincinna) hellenica* Westerlund, 1898. However, since Schütt (1980) designated a neotype for Schmidt's species, its identity is without problems.

Another Greek entity, *Horatia* (*Daphniola*)

exigua pangaea Reischütz, 1984, has been assigned to *Daphniola*. As the anatomy of this entity has never been studied, its inclusion in this genus requires confirmation.

Erythropomatiana Radoman, 1978

Erythropomatiana Radoman, 1978: 35.
Type Species: *Valvata erythropomatia* Hauffen, 1856, by original designation.

Erythropomatiana erythropomatia (Hauffen, 1856)

Valvata erythropomatia Hauffen, 1856: 465.
Type Locality: "Görzaher Grotte (Gorižane)" [="Babja Luknja" cave], Slovenia.
Type Material: type material is in the "Versammlung der Musealmitglieder des Laibacher Museums," Ljubljana, Slovenia (Hauffen, 1856).

Material Examined

- "Babja Luknja" cave, S. 35, Goričane, Medvode, Slovenia, 33T VM 51, M. Bodon leg. 16.6.1985 (2 females).
- Spring below "Babja Luknja" cave, fed by waters from the same cave, Goričane, Medvode, Slovenia, 33T VM 51, M. Bodon leg. 16.6.1985 (1 male, 3 females, 10 shells).
- "Marijno Brezno" or "Velika Gipsovka" cave, S. 6, Škofja Loka, Slovenia, 33T VM 4613, F. Stoch leg. 11.1.1998 (1 juv. specimen).

Description

Shell very small, valvatiform, thin, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire rather flat, consisting of 2.75–3.25 rather rapidly growing convex whorls; last whorl dilated, slightly descending near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, thin, slightly reflected only at columellar margin (Figs. 12, 17; Radoman, 1978: 35–36, pl. 5, figs. 18–19; 1983: 123, pl. 9, fig. 146, tab. 7; Bole & Velkovrh, 1986: fig. 18). Dimensions: height = 0.73–1.13 mm; diameter = 1.17–1.55 mm.

Operculum thin, yellowish, paucispiral, slightly thickened but without outgrowth on inner face (Figs. 18, 35; Radoman, 1978: 35; 1983: 123; Bole, 1993: 8, fig. 2B).

Body unpigmented; eye spots usually absent (only one out of six specimens examined had eye spots) (Fig. 19; Bole, 1963: 121).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather short, flat, with apex blunt and 2–3 (or one, according to Bole, 1993: fig. 1C), small, rather evident knob-like lobes on left side near apex; penial duct zig-zagging through central portion of penis to open at penis tip; large oval mass of refringent cells inside penis apex to right of penial duct; terminal portion of penial duct (immediately before opening) with very small stylet (Figs. 20, 22; Radoman, 1978: 35, fig. 6; 1983: 123, fig. 68; Bole, 1993: 8, fig. 1C).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle, very small and with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, small but slightly longer than seminal receptacle, not or slightly dilated at apex, arising very close to point at which oviduct enters albumen gland portion of pallial oviduct; seminal groove running along entire ventral side of capsule gland (Fig. 21; Radoman, 1978: 35, fig. 6; 1983: 123, fig. 68; Bole, 1993: 8, fig 1B).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 11–13 denticles, central of which longer larger; first marginal teeth rake-shaped with long lateral wing and elongated cutting edge with long row of 23–25 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like cutting edge, its cutting edge carrying rather long row of 15–19 very small denticles (Figs. 44–45; Radoman, 1978: 35; Bole, 1993: 8, fig. 2A).

Stomach without posterior caecum; intestine with well developed, tightly coiled, S-like bend on pallial wall (Figs. 20, 21; Bole, 1963: 122, fig. 2B; Radoman, 1978: 35; 1983: 40).

Osphradium variable in size, oval or elongated, kidney-shaped; ctenidium consisting of 6–11 lamellae (Figs. 20, 21; Bole, 1963: fig. 3C; 1993: 8, fig. 1A).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1978: 35; 1983: 123).

Taxonomy

Erythropomatiana is here considered a junior synonym of *Hauffenia* Pollonera, 1898 (see "The status and relationships of *Hauffenia*"). Radoman (1978) introduced this genus for *Valvata erythropomatia* Hauffen, 1856. Although the anatomy of this species was nearly the same as that of the *Hauffenia* species, *Erythropomatiana* was regarded as distinct from the latter by Radoman (1983), Bole & Velkrovh (1986), and Bole (1993).

Radoman (1978) included in *Erythropomatiana* another species from a different site, *E. verdica* Radoman, 1978, distinguished only by shell characters. This species is here recognized as a junior synonym of *Hauffenia subpiscinalis* (Kuškčer, 1932) (see below).

Fissuria Boeters, 1981

Fissuria Boeters, 1981: 57–58.
Type Species: *Fissuria boui* Boeters, 1981, by original designation.

Fissuria boui Boeters, 1981

Fissuria boui Boeters, 1981: 58–59, figs. 5–9, pl. 6, figs. 5–7.
Type Locality: "Frankreich, Dép. Vaucluse bzw. Bouches du Rhône, Durance-Grundwasser".
Type Material: the holotype (SMF 253580) is at the Senckenberg-Museum, Frankfurt am Main, Germany; paratypes are at the Senckenberg-Museum, Frankfurt am Main, Germany (SMF 253581), at the Nationaal Natuurhistorisch Museum, Leiden, The Nederlands, and in the Boeters collection (124, 418, 761), München, Germany (Boeters, 1981).

Material Examined

- Fontaine de Vaucluse, Vaucluse, France, M. Bodon leg. 1.12.1984, 22.6.1989 (3 males, 6 females, 8 shells).
- Debris of Durance River near Orgon, Bouches du Rhône, France, M. Bodon leg. 1.12.1984 (28 shells).
- La Foux spring, Draguignan (Var, France), 32T KP 92, M. Bodon leg. 7.1.1990 (4 males, 4 females, many shells).
- Spring at the Gorges Mal Infernet, Agay, Var, France, 32T LP 21, M. Bodon leg. 31.12.1990 (2 males, 11 females).
- Source du Vivier, N.D. de Vaucluse, Auribeau-sur-Siagne, Alpes Maritimes, France, 32T LP 3231, M. Bodon leg. 1.1.1991 (5 males, 5 females, many shells).
- La Fouan spring, Châteneuf Grasse, Alpes Maritimes, France, 32T LP 3737, M. Bodon, E. Bo & M. Sosso leg. 11.2.1994 (6 males, 9 females, many shells).
- Source de la Foux, Mouans-Sartoux, Alpes Maritimes, France, M. Bodon leg. 2.1.1999 (2 females, many shells).
- Alluvial springs in the bed of the Var River, on the right bank, 100–200 m upstream of wells, la Tuilière, St-Laurent du Var, Alpes Maritimes, France, M. Bodon leg. 2.1.1999 (3 males, 1 shell).

Description

Shell very small, valvatiform, thin, whitish, glassy, transparent when fresh; surface of protoconch malleated; spire from well raised to almost flat, consisting of 2.75–3.5 rather rapidly growing convex whorls; last whorl rather large, slightly dilated descending near aperture; umbilicus of variable width; aperture prosocline, roundish to ovoid; peristome complete, rather thin, slightly reflected only at lower and columellar margin (Figs. 13, 23; Boeters, 1981: 58, pl. 6, figs. 5–7). Dimensions: height = 1.19–1.61 mm; diameter = 0.93–1.77 mm.

Operculum thin, yellowish, paucispiral, not thickened and without outgrowth on inner face (Fig. 26).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent (Fig. 24).

Male genitalia with prostate gland slightly bulging into pallial cavity; penis rather short, flat, with apex pointed and 3–4 (rarely 2) more or less evident raised lobes containing mass of glandular tissue; lobes of variable size and position: usually two lobes on left side and one on ventral side at about 2/3 of penis length; sometimes also one lobe on dorsal side near base of penis); penial duct zig-zagging through right portion of penis to open at penis tip (Figs. 25, 30–34; Boeters, 1981: 57–58, figs. 5–8).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal and distal seminal re-

ceptacles more or less equal in size; bursa copulatrix variable, from very small (Boeters, 1981) to rather large, oval, with proportionally more or less elongated, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Figs. 27–29; Boeters, 1981: 57–58, fig. 9).

Radula with central tooth trapezoidal with long lateral wings and basal tongue; anterior margin with 9–11 denticles, central of which longer and larger; two basal cusps, outer of which very small, at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–11 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 22–26 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish spoon-like apex, its cutting edge carrying rather long row of 20–24 very small denticles (Figs. 46, 47).

Stomach without posterior caecum; intestine with rather developed, tightly coiled, S-like bend on pallial wall (Figs. 25, 27; Boeters, 1981, fig. 8).

Osphradium variable in size, more or less elongated, oval or kidney-shaped; ctenidium consisting of 6–13 lamellae (Figs. 25, 27).

Nervous system unknown.

Taxonomy

The genus *Fissuria* is characterized by: shell very small, valvatiform; operculum without peg; penis with 2–4 glandular lobes; female genitalia with two seminal receptacles equal in size and bursa copulatrix oval and of variable size, with anterior duct; central tooth with two pairs of basal cusps.

Beyond the type species, *Fissuria* includes an undescribed species from Liguria, Italy (Pezzoli, 1988a; Bodon et al., 1995b). Other two additional species are tentatively assigned to this genus: "*Fissuria*" *planospira* Bodon, Cianfanelli & Talenti, 1997, from Tuscany, Italy, by Bodon et al. (1997) and *Horatia* (*Hauffenia*) *raehlei* Schütt, 1980, from Cephalonia I., Greece, in this paper (see below).

Gocea Hadžišče, 1956

Gocea Hadžišče, 1956: 496–499.

Type Species: *Gocea ohridana* Hadžišče, 1956, by original designation.

Gocea ohridana Hadžišče, 1956

Gocea ohridana Hadžišče, 1956: 496–499, figs. 1–4.

Type Locality: "Ohridsee. Die Schnecke lebt in einem bis jetzt fast ununtersuchten Biotop des Sees, nämlich an den steinigen Zonen der litoralen Region, und zwar nicht an den oberflächigen Steinen, sondern tiefer unten an solchen . . .", Macedonia. According to Radoman (1983: 81) the type locality is: "Lake Ohrid on the stones by Veli Dab, spreading the east lake bank".

Type Material: Hadžišče (1956) did not give any information about the type material.

Material Examined

– Trepcja south of Ohrid, Lake Ohrid, Macedonia, 34T DL 83, *ex* W. J. M. Maassen collection (2 shells with dried soft parts).

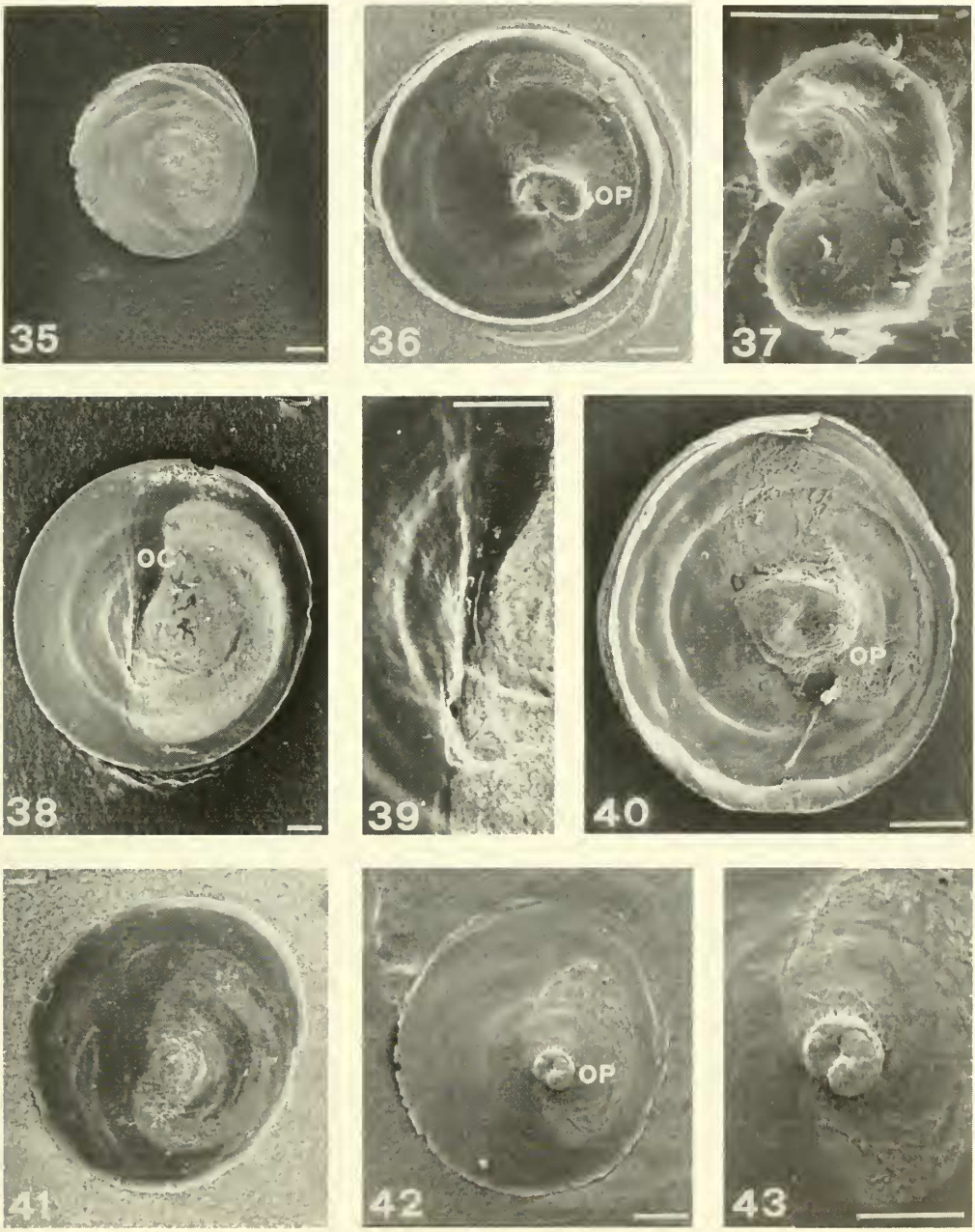
Description

Shell very small, valvatiform, ram-horn-like, partly despiralized; surface of protoconch pitted; spire from rather raised to almost flat, consisting of 2.75–3.25 rather rapidly growing convex whorls; last whorl large, despiralized, descending; umbilicus (in spiralized part of shell) rather large; aperture prosocline, irregularly pyriform due to sinuous contour (upper margin extended forward, angled at upper vertex; external margin convex, very slightly angled at periphery; lower margin slightly extended forward; columellar margin concave); peristome complete, thin, slightly reflected only at columellar margin (Fig. 53; Hadžišče, 1956: 496–497, 499, figs. 1a–b, 2a; Hadžišče et al., 1976: 2–3, figs. 1–4; Maassen, 1980: pl. 17, figs. 29–30; Radoman, 1983: 81, pl. 5, figs. 79, 80; Bole & Velkovrh, 1986: fig. 20). Dimensions: height = 0.55–0.85 mm; diameter = 1.20–1.60 (Hadžišče, 1956: 499); height = 0.53–0.85 mm; diameter = 0.60–1.55 mm (Radoman, 1983: 203, table 5).

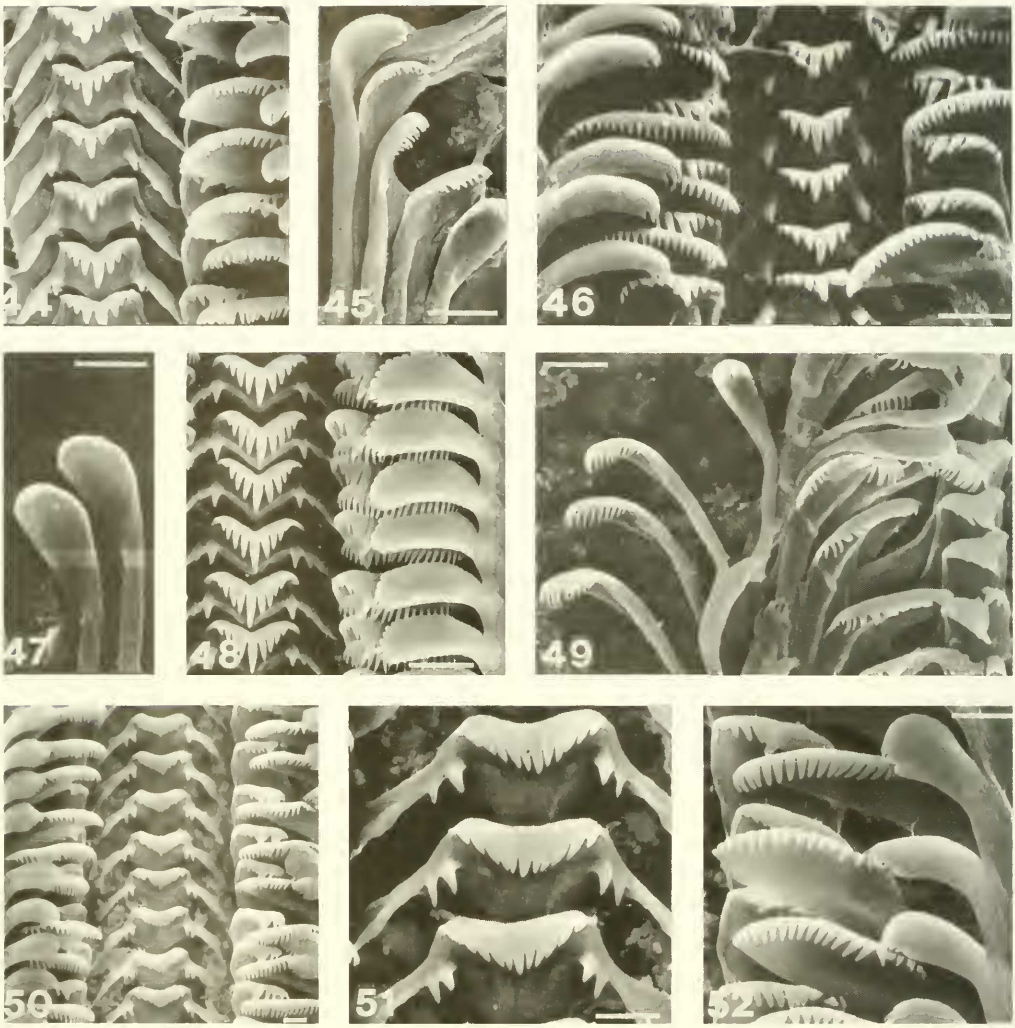
Operculum reddish, multispiral and peculiarly spiralized on outer face to resemble screw; foot tissue penetrating hole at centre of inner face (Fig. 54; Hadžišče, 1956: 497–498, fig. 2b; Hadžišče, 1959: 87; Hadžišče et al., 1976, fig. 1; Radoman, 1983: 81, fig. 42A).

Body slightly pigmented; eye spots present (Hadžišče, 1956, fig. 4).

Male genitalia with penis elongated and rather pointed, with slightly raised but evident



FIGS. 35–43. Operculum and opercular structures of *Hauffenia erythropomatia* (Hauffen, 1856) from the spring below "Babja Luknja" cave, Goričane, Medvode, Slovenia, M. Bodon leg. 16.6.1985 (Fig. 35); *Hauffenia tellinii* (Pollonera, 1898) from the spring Perilo, near Robič, Nadiža valley, Slovenia, M. Bodon leg. 9.6.1995 (Figs. 36, 37); *Kerkia kusceri* (Bole, 1961) from the spring of the Krka River, Krka, Slovenia, M. Bodon leg. 16.6.1985 (Figs. 38, 39); *Pseudohoratia ochridana* (Polinski, 1929) from Lake Ohrid, Macedonia, *ex* P. Radoman collection (Fig. 40), *Hauffenia subpiscinalis* (Kuščer, 1932) from the "Želše Jame" caves, S. 576, near Rakek, Slovenia, 3.3.1966, *ex* F. Velkovrh collection (Fig. 41) and *Hauffenia wagneri* (Kuščer, 1928) from the spring of the "Vranja peč" cave, Boštanj, Sevnica, Kršo, Slovenia, M. Bodon leg. 14.6.1985 (Figs. 42, 43). Figs. 35, 36, 38, 40–42: inner face of operculum; Figs. 37, 43: detail of opercular peg; Fig. 39: detail of opercular crest. Scale bar = 100 μm.

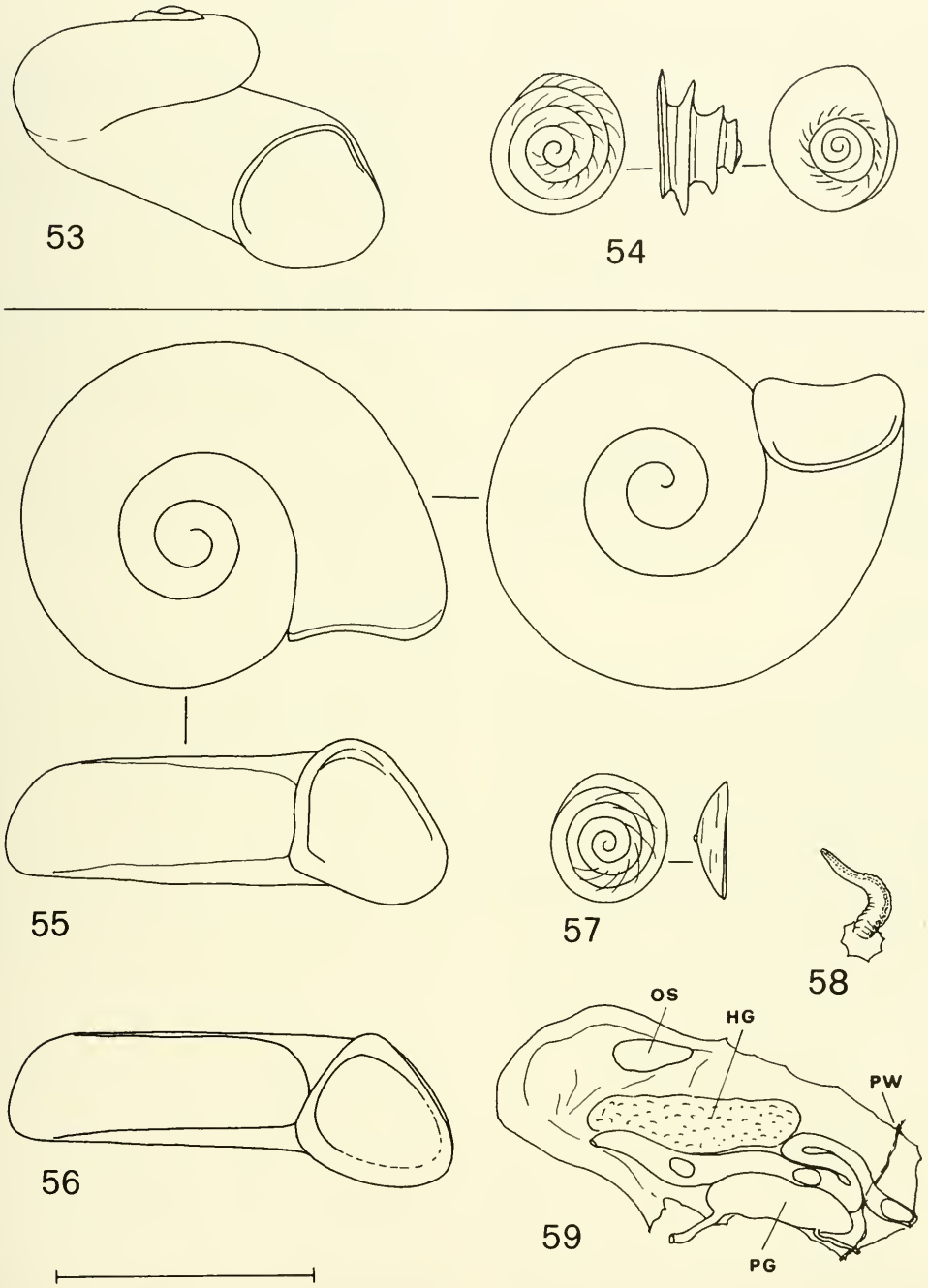


FIGS. 44–52. Radula of *Hauffenia erythropomatia* (Hauffen, 1856) from "Babja Luknja" cave, S. 35, Goričane, Medvode, Slovenia, M. Bodon leg. 16.6.1985 (Figs. 44, 45), *Fissuria boui* Boeters, 1981, from Fontaine de Vaucluse, Vaucluse, France, M. Bodon leg. 1.12.1984 (Figs. 46, 47), *Hauffenia tellinii* (Pollonera, 1898) from the spring between Spagnut and Biacis, upper Natisone valley, Pulfero, Udine, Friuli-Venetia Julia, Italy, M. Bodon leg. 9.6.1985 (Figs. 48, 49) and *Hauffenia subpiscinalis* (Kuščer, 1932) from the spring Obrh, Gorenje Jezero, Cerknica, Slovenia, M. Bodon leg. 19.6.1985 (Figs. 50–52). Figs. 44, 46, 48, 50: central part of radula; Figs. 45, 47: outer marginal teeth; Figs. 49, 52: lateral, inner and outer marginal teeth; Fig. 51: three central teeth. Scale bar = 5 μm.

lobe on left side near apex (as deduced from Hadžišče, 1956: 499, fig. 4a, and from Radoman's, 1983; fig. 42D; but according to Radoman's, 1983, description: "penis long, cylindrical, smooth, without any outgrowth") (Hadžišče, 1956: 499, fig. 4a; Radoman, 1983: 81, fig. 42D).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal and distal seminal receptacles about same size; bursa copulatrix large, kidney-shaped, with long slender duct entering bursa on anterior side; seminal groove running all along ventral side of capsule gland (Radoman, 1983: 81, fig. 42B, C).

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle



FIGS. 53–59. Shell and operculum of *Gocea ohridana* Hadžišče, 1956, from Trepcja south of Ohrid, Lake Ohrid, Macedonia, *ex* W. J. M. Maassen collection (Figs. 53, 54) and shell, operculum and anatomical details of *Hadziella ephippiostoma* Kuščer, 1932, from the Močilnik springs, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985 (Fig. 55) and the spring at Ložice, Deskle, Soča [Isonzo] valley, Slovenia, M. Bodon leg. 10.7.1996 (Figs. 56–59). Figs, 53, 55–56: shell; Figs. 54, 57: outer face (left), profile (centre in Fig. 54; right in Fig. 57) and inner face (right in Fig. 54) of operculum; Fig. 58: penis; Fig. 59: male genitalia (penis and testis excluded), intestine and pallial organs. Scale bar = 1 mm.

and 4–5 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–11 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of about 20 denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish spoon-like apex, its cutting edge carrying rather long row of small denticles (Hadžišče, 1956: 498, fig. 3; Hadžišče et al., 1976: 13, figs. 18, 19).

Stomach without posterior caecum; intestine unknown (Radoman, 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and somewhat shorter pleuro-suboesophageal connectives (Radoman, 1983: 81).

Taxonomy

Gocea is here considered a distinct genus. However some of its anatomical details are unknown, and its relationships to other Balkan genera require further study. *Gocea* is characterized: by shell very small, valvatiform, ram-horn-like, partly despiralized; operculum without peg but spiralized on outer face to resemble screw; penis with one simple lobe; female genitalia with two seminal receptacles equal in size and large, kidney-shaped bursa copulatrix with anterior duct; central tooth with one pair of basal cusps.

It includes only the type species, which is endemic to Lake Ohrid.

Hadziella Kuščer, 1932

Hadziella Kuščer, 1932: 54.

Type Species: *Hadziella ephippiostoma* Kuščer, 1932, by monotypy.

Hadziella ephippiostoma Kuščer, 1932

Hadziella ephippiostoma Kuščer, 1932: 54–55, pl. 3, figs. 4a, b.

Type Locality: "Quelle bei Podgora", Ljubljanica basin, Slovenia.

Type Material: holotype (2004a) in the Kuščer collection, Institute of Biology, University of Ljubljana, Ljubljana, Slovenia (Kuščer, 1932).

Material Examined

- Močilnik springs, Vrhnika. Plentiful karstic springs which feed the Ljubljanica River, Slovenia, 33T VL 49, M. Bodon leg. 17.6.1985 (32 shells).
- Springs near the right bank of Verd Stream, upstream of Verd village, Vrhnika. Plentiful karstic springs, Slovenia, 33T VL 48, M. Bodon leg. 17.6.1985 (9 shells).
- Obrh spring, Gorenje Jezero, Cerknica. Plentiful karstic spring in the Cerkniško Lake basin (the waters flow underground to feed the Rak River), Slovenia, 33T VL 56, M. Bodon leg. 19.6.1985 (6 shells).
- Cemun spring, Gorenje Jezero, Cerknica, Slovenia, 33T VL 56, M. Bodon leg. 19.6.1985 (3 shells).
- Spring near Ložice, along road to Kanal, Soča valley, Slovenia, 33T UM 9201, M. Bodon leg. 10.7.1996 (1 male, many shells).

Description

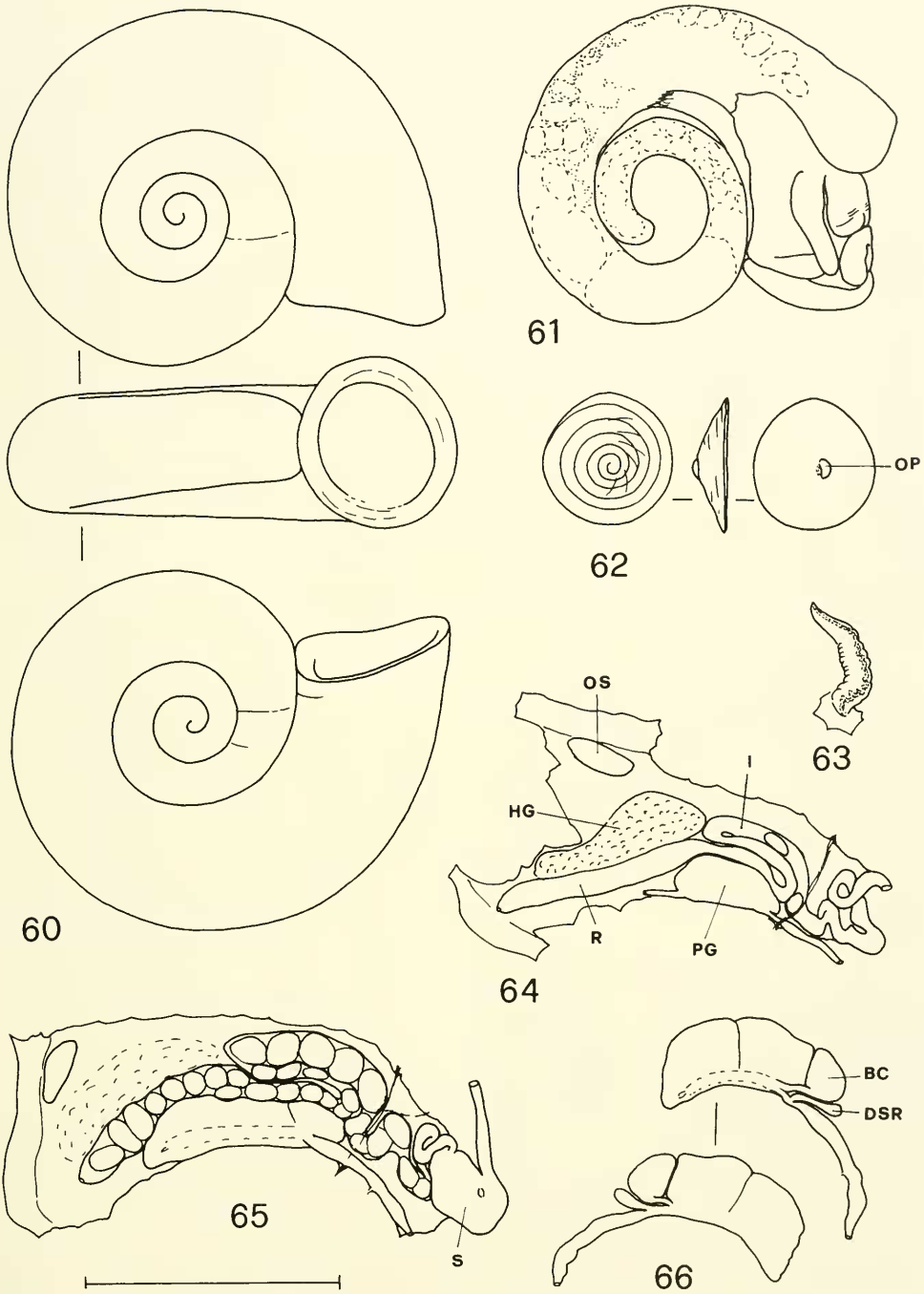
Shell very small, planispiral, concave on both sides, whitish, glassy, transparent when fresh; microsculpture of protoconch consisting of spiral rows of minute, more or less elongated knobs; spire flat, consisting of 3–3.25 rather rapidly growing whorls; external wall of last whorl flat obliquely with sort of obtuse keel at base, large, dilated, descending slightly near aperture; aperture prosocline, oval-triangular (slightly angled between columellar and external, external and lower and lower and columellar margin); peristome complete, thickened, reflected (Figs. 14, 55, 56; Kuščer, 1932: 54–55, pl. 3, figs. 4a, b; Bole, 1963: 124, Fig. 4A, B; Maassen, 1975: pl. 27, figs. 9, 10; Bole & Velkovrh, 1986: fig. 21). Dimensions: height = 0.51–0.56 mm; diameter = 1.43–1.75 mm.

Operculum thin, multispiral, concave, with very reduced outgrowth at centre of inner face (Fig. 57; Bole, 1993: 13, 15, fig. 3D).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent.

Male genitalia with entire prostate gland bulging into pallial cavity; penis slightly elongated, conical, with sides corrugated, tapering near apex, ending in pointed tip; penial duct zig-zagging through right portion of penis to open at penis tip (Figs. 58, 59; Bole, 1993: 13, 15, fig. 3C).

Female genitalia with only one (?) sac-like structure (bursa copulatrix) arising from distal



FIGS. 60–66. Shell, operculum and anatomical details of *Hadziella anti* Schütt, 1960, from the "Bus de l'Ors" cave, no. 64 FR, Cornappo valley, Udine, Friuli-Venetia Julia, Italy, 33T UM 6923, M. Bodon & F. Stoch leg. 23.7.96. Fig. 60: shell; Fig. 61: body of a female with pallial cavity open to show head; Fig. 62: outer face (left), profile (centre) and inner face (right) of operculum; Fig. 63: dorsal side of penis; Fig. 64: male genitalia (penis and testis excluded), intestine and pallial organs; Figs. 65, 66: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

renal oviduct; bursa copulatrix large, shoe-shaped, with rather long, wide duct entering bursa on posteroventral side; seminal receptacle absent (?): according to Bole (1993), its function carried out by portion of renal oviduct level with end of loop (from where proximal seminal receptacle usually arises); seminal groove running along ventral side of capsule gland (Bole, 1993: 13, 15, fig. 3C).

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin with long robust central denticle and about 4 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with many small denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of small denticles anteriorly; second marginal teeth scraper-shaped, with long and slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Bole, 1993: 13, 15, fig. 3E).

Stomach without posterior caecum; intestine with a twisted bend near the style sac and well developed, tightly coiled, Z-like bend on pallial wall (Fig. 59; Bole, 1993: 13, 15, fig. 3B).

Osphradium oval; hypobranchial gland well developed; ctenidium absent (Fig. 59; Bole, 1993: 13, 15, fig. 3A).

Nervous system unknown.

Taxonomy

The genus *Hadziella* is characterized by: shell very small, planispiral, concave on both sides; operculum with very reduced peg; penis without lobes; female genitalia with distal seminal receptacle and large, shoe-shaped bursa copulatrix with posteroventral duct; central tooth with one pair of basal cusps.

The description of the female anatomy of *Hadziella* is entirely based on Bole's (1993) study of the type species. Dissection of females of *H. anti* (Figs. 60–66) confirmed some of the characters ascertained by Bole (1993) (bursa copulatrix large, shoe-shaped, duct entering bursa on posteroventral side), but also revealed others that were not described (pallial oviduct and bursa copulatrix entirely inside the pallial cavity). Some characters seem to distinguish *H. anti* (oviduct loop absent; seminal receptacle arising from renal oviduct close to point from where duct of bursa copulatrix arises) from *H. ephippiostoma*. Because *H. anti* and *H. ephippiostoma* are closely related (they share many shell and anatomical characters), the seminal receptacle and oviduct loop are presumably similar as well. The type species should therefore be reinvestigated.

Apart from the type species, *Hadziella* includes six other species from northeastern Italy and the northwestern Balkans: *H. anti* Schütt, 1960; *H. deminuta* Bole, 1961; *H. krkae* Bole, 1992; *H. rudnicae* Bole, 1992; *H. sketi* Bole, 1961; and *H. thermalis* Bole, 1992 (Bole & Velkovrh, 1986; Bole, 1992); another undescribed entity is cited by Bole & Velkovrh (1986).

Hauffenia Pollonera, 1898

Hauffenia Pollonera, 1898: 3, as a subgenus of *Horatia*.

Type Species: *Horatia* (*Hauffenia*) *tellinii* Pollonera, 1898, by subsequent designation (Walker, 1918).

Hauffenia tellinii (Pollonera, 1898)

Horatia (*Hauffenia*) *tellinii* Pollonera, 1898: 3–4, fig. 2.

Type Locality: "L'alta valle del Natisone nel Friuli", Italy.

Type Material: Pollonera (1898) did not give any information about the type material. The Pollonera collection is at the Museo Regionale di Scienze Naturali di Torino, but the syntypes of this species have not been traced (E. Gavetti, *pers. com.*, 27.11.1997).

Horatia (*Hauffenia*) *valvataeformis* Pollonera, 1898: 3–4, fig. 3.

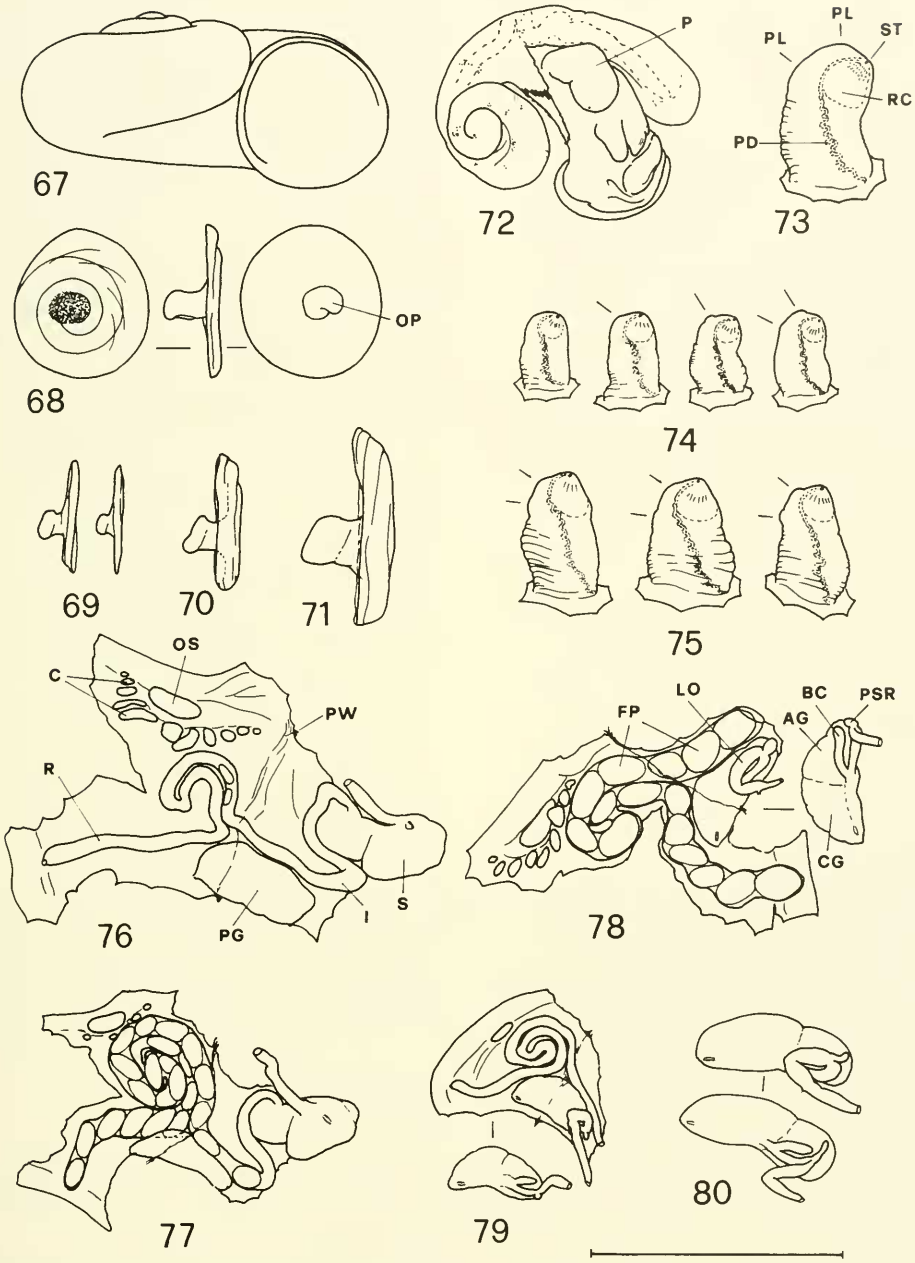
Type Locality: "l'alta valle del Natisone nel Friuli", Italy.

Type Material: Pollonera (1898) did not give any information about the type material. The Pollonera collection is at the Museo Regionale di Scienze Naturali di Torino, but the syntypes of this nominal taxon have not been traced (E. Gavetti, *pers. com.*, 27.11.1997).

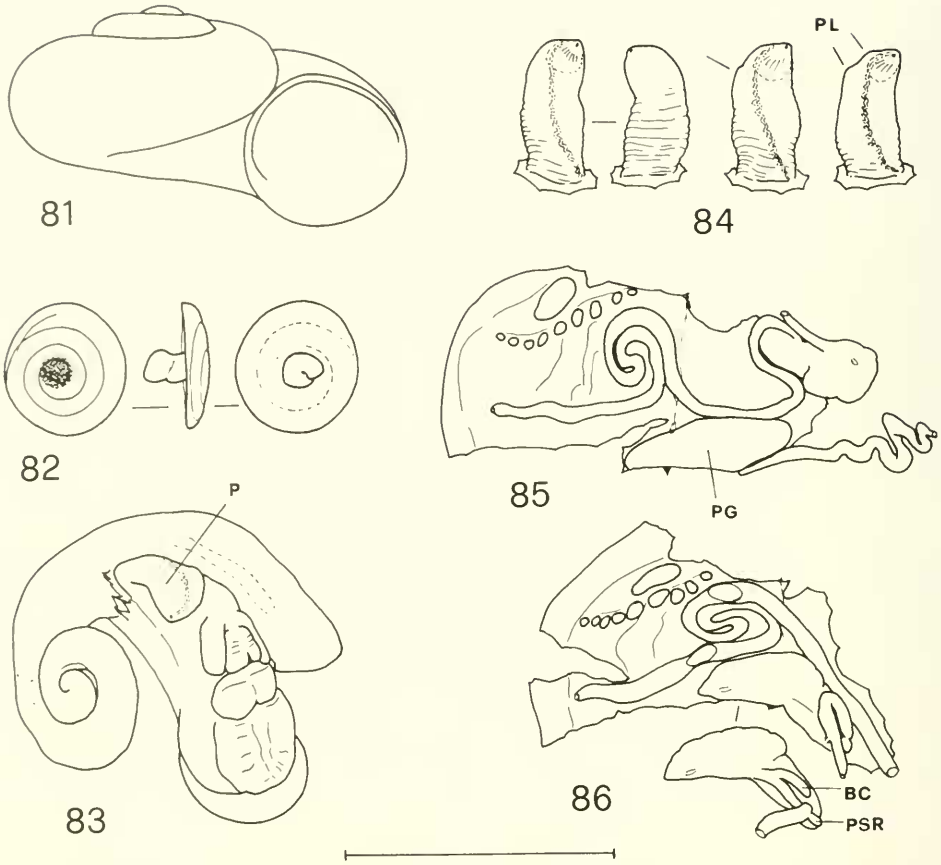
Hauffenia michleri Kuščer, 1932: 56–57, pl. 5, fig. 3.

Type Locality: "Ljubljanica quellen Močilnik", Slovenia.

Type Material: holotype (2005a) in the Kuščer collection, "Zoologischen Institut der Uni-



FIGS. 67–80. Shell, operculum and anatomical details of *Hauffenia tellinii* (Pollonera, 1898) from debris of Natisone River, Paderno, Premariacco, Udine, Friuli-Venetia Julia, Italy, M. M. Giovannelli leg. 5. 1988 (Figs. 67, 70), from the spring Perilo, near Robič, Nadiža valley, Slovenia, M. Bodon leg. 9.6.1995 (Figs. 68, 80), from the spring between Spagnut and Biacis, upper Natisone valley, Pulfero, Udine, Friuli-Venetia Julia, Italy, M. Bodon leg. 23.9.1993, 9.6.1985 (Figs. 69, 72–74, 77, 79), from the spring at Tarpezzo, Alberone valley, S. Pietro al Natisone, Udine, Friuli-Venetia Julia, Italy, M. Bodon leg. 1.4.1991 (Fig. 71) and from the springs of Timavo River, S. Giovanni al Timavo, Duino-Aurisina, Trieste, Friuli-Venetia Julia, Italy, M. Bodon leg. 31.3.1991 (Figs. 75, 76, 78). Fig. 67: shell; Figs. 68–71: outer face (Fig. 68 left), profile (Fig. 68 centre; Figs. 69–71) and inner face (Fig. 68 right) of operculum; Fig. 72: body of a male with pallial cavity open to show head and penis; Figs. 73–75: dorsal side of penis of eight males; Figs. 76, 77: prostate gland, stomach, intestine and pallial organs of two males; Figs. 78, 79: renal and pallial oviduct, intestine and pallial organs of two females; Fig. 80: renal and pallial oviduct of a female. Scale bar = 1 mm (67–72, 74–80); = 0.5 mm (73).



FIGS. 81–86. Shell, operculum and anatomical details of *Hauffenia michleri* Kuščer, 1932, (junior synonym of *H. tellinii*) from the Močilnik springs, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985 (Fig. 81) and the spring on right bank of the Verd brook, near the Verd spring, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985 (Figs. 82–86). Fig. 81: shell; Fig. 82: outer face (left), profile (centre) and inner face (right) of operculum; Fig. 83: body of a male with pallial cavity open to show head and penis; Fig. 84: dorsal side (first picture on left and last two on right) and ventral side (second picture) of penis of three males; Fig. 85: prostate gland, stomach, intestine and pallial organs of a male; Fig. 86: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

versität Ljubljana", Slovenia (Kuščer, 1932).

Material Examined

– Perilo spring, Robič, upper Nadiža [Natisone] valley, Slovenia, 33T UM 8522, M. Bodon leg. 9.6.1995 (1 female, many shells).
– Alluvial springs on left bank of the Nadiža River, 250 m upstream from the gorge, Hurja, Potoki, Slovenia, 33T UM 8323, M. Bodon, S. Cianfanelli & G. Manganelli leg. 25.7.1996 (1 male, 1 female, 4 shells).
– Alluvial springs on the right bank of the Nadiža River, at the km 37 milestone on the road to Kobarid, Slovenia, 33T UM 8422, M. Bodon & I. Mišič leg. 15.7.1996 (1 male).
– Plentiful spring 1.1 km from the Italy-Slovenia border, welling out below the road in the upper Natisone valley (Pulfero, Udine, Friuli-Venetia Julia, Italy), 33T UM

8318, M. Bodon leg. 1.4.1991 (1 female, many shells).

– Spring between Spagnut and Biacis, upper Natisone valley, Pulfero, Udine, Friuli-Venetia Julia, Italy, 33T UM 8211, M. Bodon leg. 23.9.1993, 9.6.1985, 1.4.1991 (11 males, 3 females, many shells) (Pezzoli, 1988a).

– Cave of S. Giovanni d'Antro no. 43 Fr, Pulfero, Udine, Friuli-Venetia Julia, Italy, 33T UM 8212, M. Bodon leg. 22.9.1983 (many shells), F. Gasparo & F. Stoch leg. 19.7.1992 (2 females, 3 shells).

– Mustig spring, Vedronza, Torre valley, Lusevera, Udine, Friuli-Venetia Julia, Italy, 33T UM 6524, M. Bodon, M. M. Giovannelli & F. Stoch leg. 22.7.1989 (1 female, 10 shells).

– Spring at Tarpezzo, Alberone valley, welling below the road and flowing through the village, S. Pietro al Natisone, Udine, Friuli-Venetia Julia, Italy, 33T UM 8411, M. Bodon leg. 8.6.1985 (4 shells), 1.4.1991 (4 males, 1 female, many shells) (Pezzoli, 1988a, cited, in part, as *Islamia* sp.).

– Plentiful spring 1 km downstream from Bodigoi, Ludrio valley, welling below the road, Prepotto, Udine, Friuli-Venetia Julia, Italy, 33T UM 8402, M. Bodon leg. 1.4.1991 (1 female, many shells).

– Spring 700 m upstream of Podresca, Ludrio valley, Prepotto, Udine, Friuli-Venetia Julia, Italy, 33T UM 8905, M. Bodon leg. 7.7.1993 (3 males, 1 female, many shells).

– Spring near Podclanz at the turn-off for Salamant, Ludrio valley, Prepotto, Udine, Friuli-Venetia Julia, Italy, 33T UM 9107, M. Bodon leg. 7.7.1993 (1 male, 1 female, many shells).

– Alluvial springs on the right bank of the Torre River, 100–200 m upstream from of the confluence of Isonzo, Papariano, Fiumicello, Udine, Friuli-Venetia Julia, Italy, 33T UL 7774, M. Bodon leg. 27.7.1996 (1 male, 5 females, 5 shells).

– Alluvial springs on the right bank of the Isonzo River, under the railway viaduct, Papariano, Fiumicello, Udine, Friuli-Venetia Julia, Italy, 33T UL 7774, M. Bodon leg. 27.7.1996 (2 males and 1 female).

– Springs of the Timavo River, S. Giovanni al Timavo, Duino-Aurisina, Trieste, Friuli-Venetia Julia, Italy, 33T UL 9071, M. Bodon leg. 31.3.1991 (6 males, 2 females, many shells) (Stammer, 1932; Pezzoli, 1988a).

– Alluvial spring near Molin del Cucco, Rivoli di Osoppo, Osoppo, Udine, Friuli-Venetia Julia, Italy, 33T UM 4921, S. Cianfanelli & M. Calcagno leg. 29.12.1998 (1 male).

– "Grotta de la Foos" cave, no. 229 Fr, Campone, Tramonti di Sotto, Pordenone, Friuli-Venetia Julia, Italy, 33T UM 3124, M. Bodon & F. Stoch leg. 7.7.1991, 15.7.1993 (1 male, 1 female, 2 shells) (Pezzoli, 1988b, 1989).

– "Grotta I Landri" cave, no. 1254 V, Colli di Conegliano, San Pietro di Feletto, Treviso, Venetia, Italy, 33T TL 8585, F. Stoch leg. 15.7.1999 (1 juv. specimen).

– Spring on the right bank of the Idrijca Stream, near Ukovnik, Spodnja Idrija, Slovenia, 33T VM 20, F. Gasparo e F. Stoch leg. 5.6.1993 (1 male, 1 female, 1 shells).

– Močilnik springs, the main Ljublianica source near Vrhnika (type locality of *Hauffenia michleri*), Slovenia, 33T VL 49, M. Bodon leg. 17.6.1985 (1 female, many shells).

– Springs on the right bank of Verd brook, Vrhnika, Slovenia, 33T VL 48, M. Bodon leg 17.6.1985 (3 males, 1 females, many shells).

Other shells with operculum were examined from the following localities:

– Spring "La Santissima" of the Livenza River, Polcenigo, Pordenone, Friuli-Venetia Julia, Italy, 33T UL 0499, M. Bodon leg. 28.3.1991 (1 shell) (Pezzoli, 1988a).

– Debris of Barcis lake, Barcis, Pordenone, Friuli-Venetia Julia, Italy, 33T UM 1318, M. Bodon leg. 8.7.1991 (1 shell).

– Spring on the right bank of a stream affluent of the Pontaiba Stream, Colle di Pinzano, Pinzano, Pordenone, Friuli-Venetia Julia, Italy, 33T UM 4118, M. Bodon & F. Stoch leg. 15.7.1993 (1 shell).

– Spring along the road upstream Casiacco, Arzino valley, Vito d'Asio, Pordenone, Friuli-Venetia Julia, Italy, 33T UM 4221, M. Bodon & F. Stoch leg. 15.7.1993 (1 shell).

– Debris of the Tagliamento River, Ponte della Delizia, Valvasone-Codroipo, Pordenone-Udine, Friuli-Venetia Julia, Italy, 33T UL 3792, M. Bodon leg. 27.4.1986 (1 shell) (Pezzoli, 1988a).

– Peschiera spring, Vedronza, Torre valley,

Lusevera, Udine, Friuli-Venetia Julia, Italy, 33T UM 6524, M. Bodon leg. 24.9.1983 (1 shell) (Pezzoli, 1988a).

– Springs on left bank of Vedronza River, Casera Morandin, Lusevera, Udine, Friuli-Venetia Julia, Italy, 33T UM 6425, M. Bodon leg. 24.9.1983 (1 shell) (Pezzoli, 1988a).

– Debris of the Natisone River, Paderno, Premariacco, Udine, Friuli-Venetia Julia, Italy, 33T UM 7600, M. M. Giovannelli, leg. 5.1988 (1 shell).

– Spring between Robič and Sužid, Slovenia, 33T UM 8721, M. Bodon leg. 9.6.1985 (1 shell).

– Springs downstream from Liessa, Cosizza valley, Grimacco, Udine, Friuli-Venetia Julia, Italy, 33T UM 9012, M. Bodon leg. 1.4.1991 (1 shell).

– Springs on right bank of the Grivò Stream, Canal di Grivò, Faedis, Udine, Friuli-Venetia Julia, Italy, 33T UM 7314, M. Bodon leg. 8.7.1983 (1 shell).

– Debris of the Isonzo River, Peteano, Sagrado d'Isonzo, Gorizia, Friuli-Venetia Julia, Italy, 33T UL 8783, M. Bodon leg. 20.6.1985 (1 shell) (Bodon & Giovannelli, 1994; Pezzoli, 1988a).

– Debris of the Isonzo River, Papariano, Fiumicello, Udine, Friuli-Venetia Julia, Italy, 33T UL 7774, M. Bodon leg. 21.9.1983, 20.6.1985 (5 shells) (Bodon & Giovannelli, 1994; Pezzoli, 1988a).

– Spring on right bank of the Idrijca Stream, upstream from Podroteja, Idrija, Slovenia, 33T VL 29, M. Bodon leg. 13.7.1996 (5 shells).

Shell material from the type locality was collected in the following place:

– Debris of the Natisone River, upstream Linder, Pulfero, Udine, Friuli-Venetia Julia, Italy, 33T UM 8216, M. Bodon leg. 23.9.1983 (8 shells) (Pezzoli, 1988a).

For other localities where only shells were collected see Pezzoli (1988a, 1996).

Description

Shell very small, valvatiform to planispiral, thin, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire from rather raised to almost flat, consisting of 2.5–3.5 rapidly growing convex whorls; last whorl large, dilated, more or less descending, sometimes slightly detached near aperture; umbilicus wide, about 1/6–1/3 of shell diameter; aperture more or less prosocline, roundish to pyriform; peristome complete, thin and not or slightly reflected only at columellar margin (Figs. 15, 16, 67, 81, 87; Pollonera, 1898: 3, figs. 2, 3, as *Horatia valvataeformis;* Kuščer, 1932: 56–57, pl. 5, fig. 3, as *Hauffenia michleri;* Bole, 1967b: 112, fig. 1A, as *Hauffenia michleri;* Bole, 1970: 4–6, fig. 1; Maassen, 1975: pl. 27, figs. 4–8, as *Hauffenia michleri;* Pezzoli et al., 1975: pls. 1, 2; Radoman, 1978: 34–35, pl. 4, figs. 13–15, as *Hauffenia michleri;* Bole, 1979: 36, figs. 1–4a, b, as *Hauffenia michleri;* Giusti & Pezzoli, 1980: 45, figs. 18B–D, 26L; Giusti & Pezzoli, 1982: pl. 1, fig. 4; Radoman, 1983: 122, table 7, pl. 9, figs. 143, 144, as *Hauffenia michleri;* Bole & Velkovrh, 1986: fig. 22; Pezzoli, 1989, pl. 5, fig. 11; Bodon & Giovannelli, 1994: fig. 4M, N). Dimensions: height = 0.45–1.20 mm; diameter = 0.98–2.30 mm.

Operculum yellowish, paucispiral, thick and with well developed spiralized peg at centre of inner face; peg variable in size in different populations, but always dilated at apex (Figs. 36, 37, 68–71, 82; Pollonera, 1898: 3, fig. 2, fig. 3, as *Horatia valvataeformis;* Bole, 1967a: 88, fig. 4(5), as *Hauffenia michleri;* Bole, 1967b: 113, fig. 1B3, as *Hauffenia michleri;* Bole, 1970: 91, fig. 2A5; Bole, 1993: 6, fig. 2B; Radoman, 1978: 33–34, as *Hauffenia michleri;* Radoman, 1983: 121–122, as *Hauffenia michleri*).

Body unpigmented (a few traces of pigment sometimes on visceral sac); eye spots absent (Figs. 72, 83; Bole, 1967a: 87–88, fig. 4(2), as *Hauffenia michleri;* Bole, 1967b: 112–113, as *Hauffenia michleri*).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather short, flat, with apex blunt and no or 1–2 slightly evident lateral lobes on left side near apex, penial duct zig-zagging through central portion of penis to open at penis tip; globular mass of refringent cells inside penis apex to right of penial duct; terminal portion of penial duct (immediately before opening) with very small stylet (Figs. 73–77, 84–85, 95–99; Bole, 1967a: 87, fig. 4(4), as *Hauffenia michleri;* Bole, 1967b: 112, fig. 1B2, as *Hauffenia michleri;* Bole, 1970: 91, fig. 2A3; Giusti & Pezzoli, 1980: 45, fig. 18E; Radoman, 1983: 120, as *Hauffenia michleri;* Bole, 1993: 6, fig. 1C, as *Hauffenia michleri*).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; the smaller structure con-

tains spermatozoa oriented with their heads anchored to cells of the wall and is thus a seminal receptacle, and the larger contains few non-oriented and partially digested spermatozoa and is thus a bursa copulatrix; seminal receptacle very small and sessile or with very short duct arising from oviduct level with end of loop; bursa copulatrix very small but markedly longer than seminal receptacle, not dilated at apex, arising very close to point at which oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Figs. 78–80, 86, 101; Bole, 1967a: 87–88, fig. 4(3), as *Hauffenia michleri;* Bole, 1970: 91, fig. 2A2; Giusti & Pezzoli, 1980: 43, fig. 18F; Radoman, 1983: 40, 120, as *Hauffenia michleri;* Bole, 1993: 6, fig. 1B; Bole, 1993: 6, as *Hauffenia michleri*).

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–13 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 16–26 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 15–18 very small denticles (Figs. 48–49; Bole, 1967a: 87, fig. 4(6), as *Hauffenia michleri;* Bole, 1967b: 112, fig. 1B4, as *Hauffenia michleri;* Bole, 1970: 91, fig. 2A4; Bole, 1993: 6, fig. 2A).

Stomach without posterior caecum; intestine with well developed, Z-like or question-mark-like bend on pallial wall (Figs. 76–79, 85–86; Radoman, 1983: 40, as *Hauffenia michleri*).

Osphradium variable in size, oval or elongated, kidney-shaped; ctenidium absent or consisting of 1–13 lamellae (Figs. 76–79, 85–86; Bole, 1967a: 87 fig 4(1), as *Hauffenia michleri;* Bole, 1967b: 112, fig. 1B1, as *Hauffenia michleri;* Bole, 1970: 91, fig. 2A1; Bole, 1993: 6, fig. 1A).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1983: 120, as *Hauffenia michleri*).

Taxonomy

Hauffenia is the second nominal genus established for the European valvatiform hydrobiids. It was introduced as a subgenus of *Horatia* Bourguignat, 1887, and raised to the rank of distinct genus by Kuščer (1932, 1933a, b). This was only demonstrated to be correct when Bole (1970) studied the type species anatomically and found its genitalia to be clearly different from those described by Radoman (1966) in the type species of *Horatia*. (For diagnosis, status and relationships of *Hauffenia* with *Erythropomatiana* Radoman, 1978, *Neohoratia* Schütt, 1961, and *Vrania* Radoman, 1978, see "Status and Relationships of Hauffenia", below.)

In the last 30 years, many valvatiform hydrobiid species from western Europe were included into *Hauffenia* (also as *Horatia* (*Hauffenia*)), often simplistically on the basis of shell characters alone, by Bole (1961), Schütt (1961b, 1980), Binder (1966) and Bernasconi (1975, 1984, 1985). Most of them are in need of revision because only the shells were studied. Some are revised and redescribed in the present paper. This revision enabled us to ascertain that geographical distribution of *Hauffenia* is limited to the northern sector of the former Yugoslavia (Slovenia and Croatia), Austria and the neighbouring areas of north-eastern Italy.

Hauffenia michleri is here recognized as junior synonym of *H. tellinii* (see taxonomic remarks to *H. tellinii* in the section on *Hauffenia* species).

Horatia Bourguignat, 1887

Horatia Bourguignat, 1887: 46, 47–49.

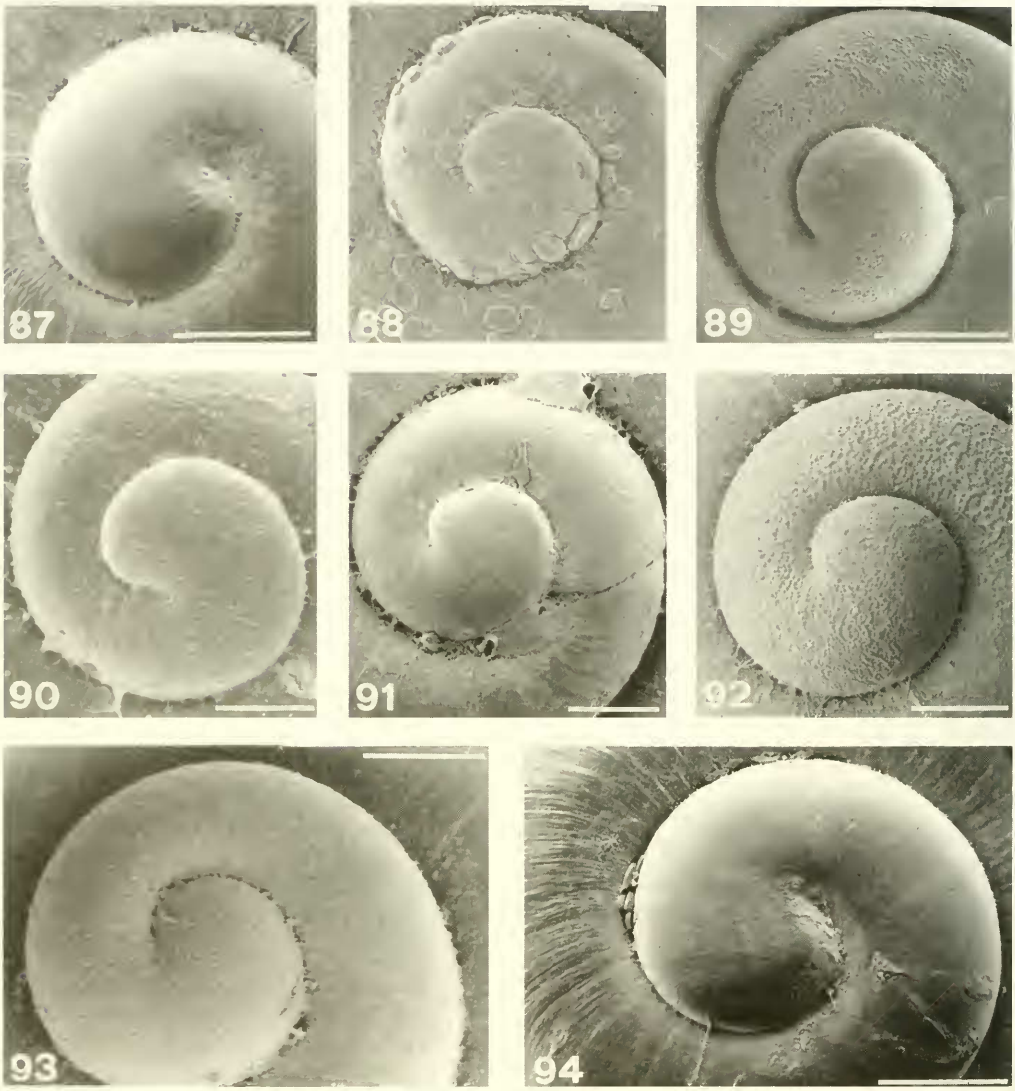
Type Species: *Horatia klecakiana* Bourguignat, 1887, by subsequent designation (Westerlund, 1902).

Horatia klecakiana Bourguignat, 1887

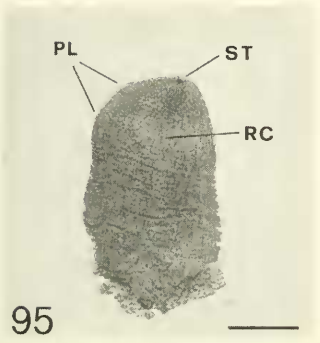
Horatia klecakiana Bourguignat, 1887: 49–50, figs. 18–21.

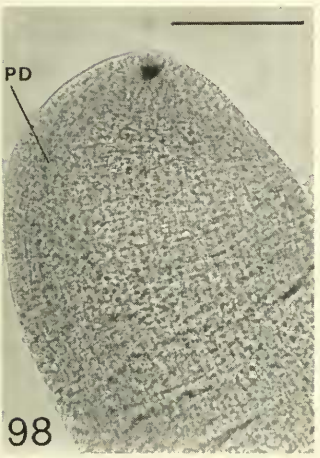
Type Locality: "sorgente près de Ribaric, dans la vallée de la Cettina", Croatia. According to Radoman (1983: 52) this corresponds to "the Vrijovac spring in the source area of the Cetina river".

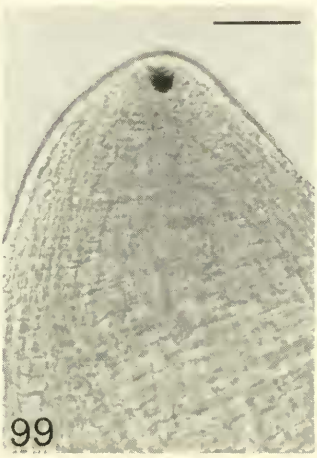
Type Material: lectotype (shell) in the Bourguignat collection, Museum d'Historie Naturelle de Genève, Geneva, Switzerland (Binder, 1957).

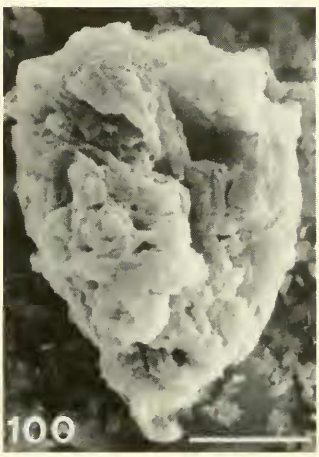


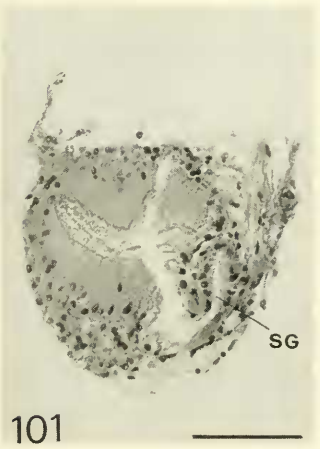
FIGS. 87–94. Microsculpture of protoconchs. Fig. 87: *Hauffenia michleri* Kuščer, 1932, (junior synonym of *H. tellinii*) from the Močilnik springs, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985; Fig. 88: *Horatia klecakiana* Bourguignat, 1887, from Cetina near Vrlika, Croatia, 16.9.1964, *ex* F. Velkovrh collection; Fig. 89: *Kerkia kusceri* (Bole, 1961) from the spring of the Krka River, Krka, Slovenia, M. Bodon leg. 16.6.1985; Fig. 90: *Hauffenia subpiscinalis* (Kuščer, 1932) from the spring Kotla, Rakov Škocjan, Slovenia, M. Bodon leg. 18.6.1985; Fig. 91: *Pezzolia radapalladis* Bodon & Giusti, 1986, from the spring inside the Rio di Tonnego, Ponte della Vittoria, Rapallo, Genova, Liguria, Italy, M. Bodon leg. 16.12.1979; Fig. 92: *Pseudohoratia ochridana* (Polinski, 1929) from Lake Ohrid, Macedonia, *ex* P. Radoman collection; Fig. 93: *Hauffenia wagneri* (Kuščer, 1928) from the spring of the "Vranja Peč" cave, Boštanj, Sevnica, Krško, Slovenia, M. Bodon leg. 14.6.1985; Fig. 94: *Hauffenia subcarinata* Bole & Velkovrh, 1987, from the spring near Ložice, along the road to Kanal, Soča valley, Slovenia, M. Bodon leg. 10.7.1996. Scale bar = 100 μm.

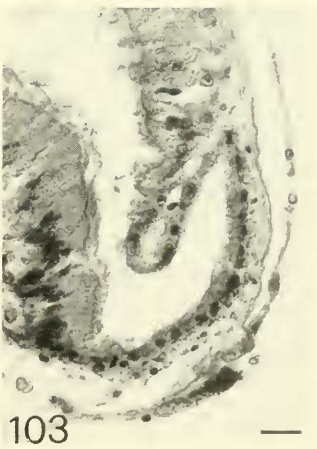




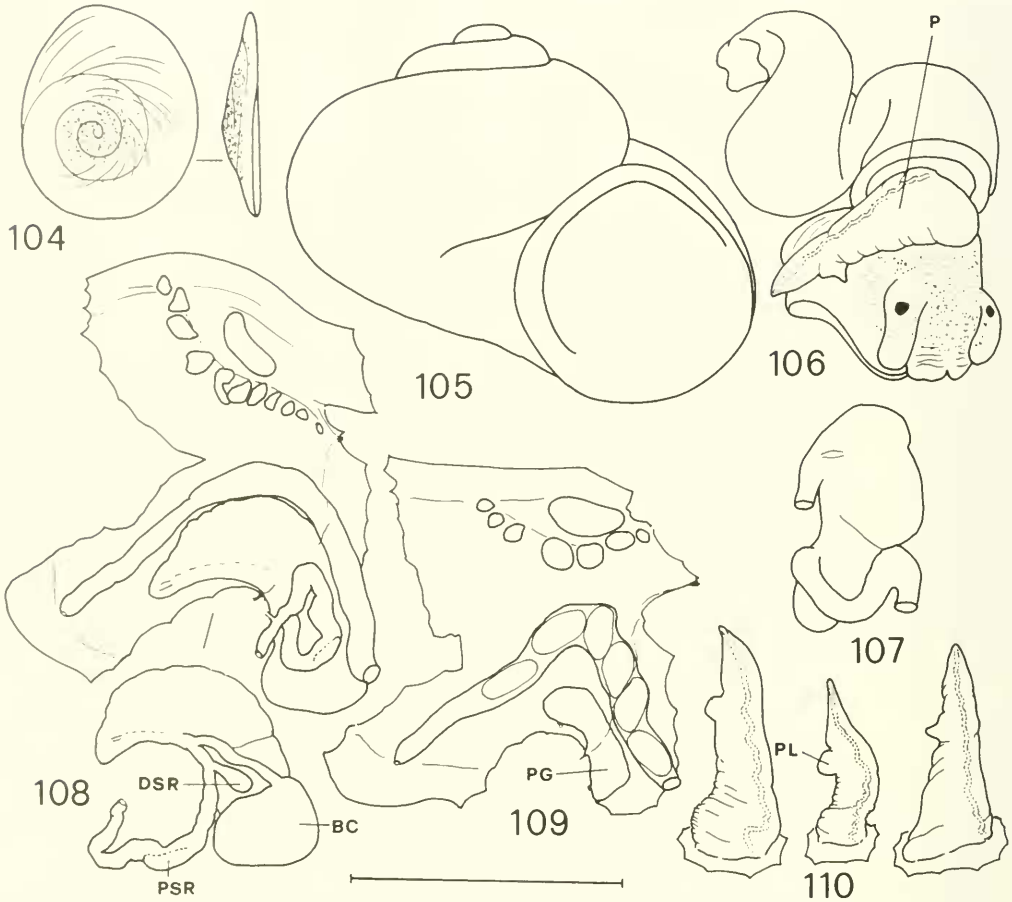








FIGS. 95–103. Penis, stylet and pallial oviduct of *Hauffenia tellinii* (Pollonera, 1898) from the spring between Spagnut and Biacis, upper Natisone valley, Pulfero, Udine, Friuli-Venetia Julia, Italy, M. Bodon leg. 23.9.1993, 1.4.1991 (Figs. 95, 96, 98, 101), *Hauffenia michleri* Kuščer, 1932, (junior synonym of *H. tellinii*) from the spring on right bank of the Verd brook, near the Verd spring, Vrhnika, Slovenia, M. Bodon leg 17.6.1985 (Figs. 97, 99), and *Hauffenia subpiscinalis* (Kuščer, 1932) from the "Želške Jame" caves, S. 576, near Rakek, Slovenia, 3.3.1966, *ex* F. Velkovrh collection (Fig. 100) and from the Močilnik springs, Vrhnika, Slovenia, M. Bodon leg. 17.6.1885 (Figs. 102, 103). Figs. 95–97: penis; Figs. 98, 99: apex of penis; Fig. 100: the entire stylet; Figs. 101, 102: section of capsule gland; Fig. 103: detail of seminal groove. Scale bar = 100 μm (95–97), 50 μm (98, 99, 101, 102), 10 μm (100, 103).



FIGS. 104–110. Operculum, shell and anatomical details of *Horatia klecakiana* Bourguignat, 1887, from Cetina near Vrlika, Croatia, 16.9.1964, *ex* F. Velkovrh collection. Fig. 104: outer face (left), and profile (right) of operculum; Fig. 105: shell; Fig. 106: body of a male with pallial cavity open to show head and penis; Fig. 107: stomach; Fig. 108: renal and pallial oviduct, intestine and pallial organs of a female; Fig. 109: prostate gland, intestine and pallial organs of a male; Fig. 110: dorsal side of penis of three males. Scale bar = 1 mm.

Material Examined

– Cetina near Vrlika, Croatia, 33T XJ, 16.9.1964, *ex* F. Velkovrh collection (3 males, 2 females, many shells).

Description

Shell very small, valvatiform to ovoid, rather robust, whitish, opaque; surface of protoconch malleated; spire more or less raised, consisting of 3.25–3.5 rather rapidly growing convex whorls; last whorl dilated and more or less descending near aperture; umbilicus not very wide; aperture prosocline, roundish to oval; peristome complete, external margin thin, columellar margin thickened, reflected (Figs. 88, 105; Bourguignat, 1887: 47–56, figs. 2, 3, as *Horatia letourneuxi,* figs. 4, 5, as *H. praeclara,* figs. 6, 7, as *H. albanica,* figs. 10, 11, as *H. obliqua,* figs. 10–13, as *H. verlikana,* figs. 14, 15, as *H. palustris,* figs. 16, 17, as *H. fontinalis,* figs. 18–23, as *H. obtusa;* Binder, 1957: 59–62, figs. 1a–r, u–w; Ant, 1962: 74, figs. 1–21, 25–30; Radoman, 1965: 143, Figs. 3, 4; Radoman, 1966: 246, fig. 2; Radoman, 1983: 52, pl. 3, fig. 38). Dimensions: height = 1.55–2.14 mm; diameter =

1.81–2.18 mm (Radoman, 1965: table 2; 1983: 201, table 3).

Operculum thin, reddish yellow, paucispiral, slightly thickened at centre, lacking outgrowth on inner face (Fig. 104; Radoman, 1965: fig. 3; Boeters, 1974: 86; Radoman, 1983: 52).

Body slightly pigmented; eye spots present (Fig. 106; Boeters, 1974: 86).

Male genitalia with prostate gland bulging well into pallial cavity; penis rather elongated and slender, with apex pointed and single or double, rather evident, lobe on left side at about 2/3 of its length; penial duct zig-zagging through lateral portion of first half of penis, becoming central before opening at penis tip (Figs. 109–110; Boeters, 1974: 86, figs. 1, 2; Radoman, 1983: 52, fig. 20).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle thin and bent to adhere to oviduct level with end of loop; distal seminal receptacle larger than proximal, wide at apex; bursa copulatrix large, kidney-shaped, with long slender duct that enters bursa on anterodorsal side; seminal groove running along ventral side of capsule gland (Fig. 108; Radoman, 1966: 249, fig. 8; 1973a: 6; Boeters, 1974: 86; Radoman, 1983: 40, 51, fig. 20).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and 5 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–11 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 25–30 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Binder, 1957: 62, fig. 2; Boeters, 1974: 86; Hershler & Longley, 1986: fig. 28C).

Stomach without posterior caecum; intestine with bend absent or relatively undeveloped (Figs. 107–109; Radoman, 1973a: 6; Boeters, 1974: 86; Radoman, 1983: 40).

Osphradium variable in size, elongated, kidney-shaped; ctenidium consisting of 7–11 lamellae (Figs. 108, 109; Boeters, 1974: 86).

Nervous system with long pleuro-supraoesophageal and rather long to somewhat short pleuro-suboesophageal connectives (Radoman, 1966: 249; 1983: 40, 51)

Taxonomy

The genus *Horatia* is characterized by: shell very small, valvatiform to ovoid; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, distal larger than proximal, and large, kidney-shaped bursa copulatrix, with anterodorsal duct; central tooth with one pair of basal cusps.

Horatia was the first nominal genus established for the European valvatiform hydrobiids. Before then, and sometimes also after, valvatiform hydrobiids were included in the heterobranch genus *Valvata* Müller, 1774.

Together with the type species, Bourguignat (1887) introduced many nominal species of *Horatia*. Apart from *Horatia servaini* Bourguignat, 1887, which is regarded as a junior synonym of *Islamia valvataeformis* (Möllendorff, 1873) (Radoman, 1983), all the others, from Dalmatia and Albania are currently regarded as junior synonyms of *Horatia klecakiana* Bourguignat, 1887 (Binder, 1957; Radoman, 1983). They are: *Horatia albanica* Bourguignat, 1887; *H. fontinalis* Bourguignat, 1887; *H. letourneuxi* Bourguignat, 1887; *H. obliqua* Bourguignat, 1887; *H. obtusa* Bourguignat, 1887; *H. palustris* Bourguignat, 1887; *H. praeclara* Bourguignat, 1887; and *H. verlikana* Bourguignat, 1887. Ant (1962) also regarded *H. knorri* Schütt, 1961, as a possible junior synonym of *H. klecakiana*, but this is very doubtful.

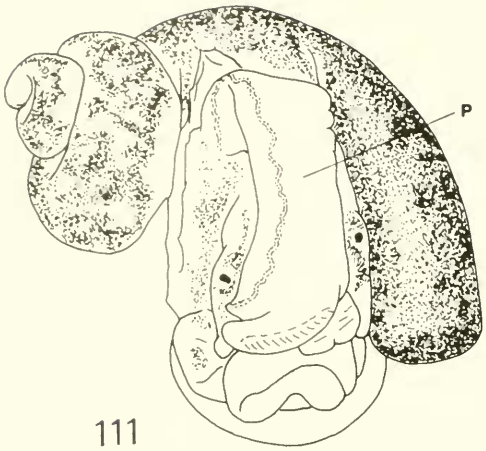
Besides the type species, *Horatia* includes two other species inhabiting different drainages from that where *H. klecakiana* lives: *H. macedonica* (Kuščer, 1936) and *H. novoselensis* Radoman, 1966, both from Macedonia (Radoman, 1983).

Reports of species of *Horatia* exist from other European and non-European countries (Willmann & Pieper, 1978; Bole & Velkovrh, 1986; Kabat & Hershler, 1993), but all of them are questionable.

Islamia Radoman, 1973a

Islamia Radoman, 1973a: 10.

Type Species: *Horatia servaini* Bourguignat, 1887, by original designation. *Horatia servaini* is a junior synonym of *Hydrobia*



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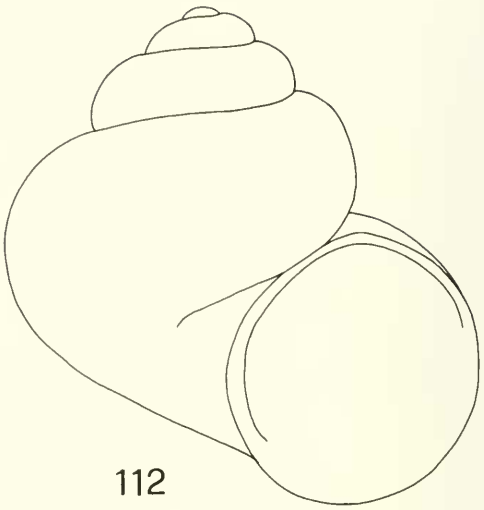

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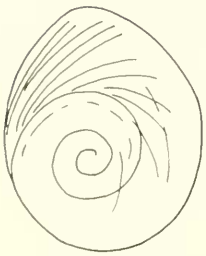

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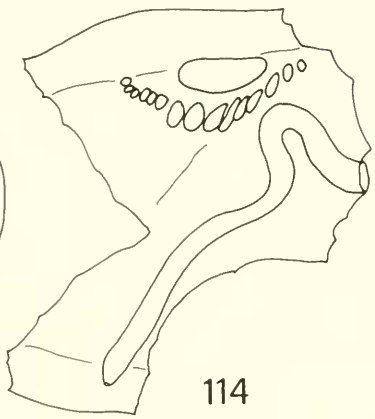

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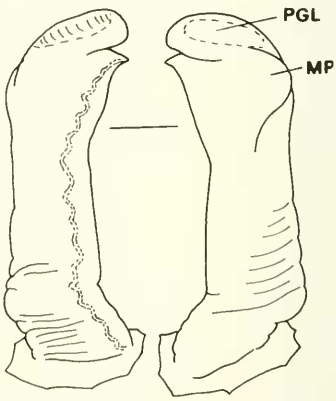

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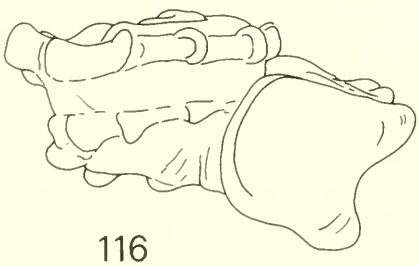

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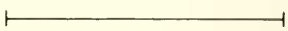


FIGS. 111–116. Shell, operculum and anatomical details of *Islamia valvataeformis* (Möllendorff, 1873) from Vrelo Bosne, Sarajevo, Bosnia, G. Vigna & A. Vigna leg. (Figs. 111–115) and shell of *Karevia ornata* (Radoman, 1957) from the harbour of Trpezjca, Lake Ohrid, Macedonia, 5.1976, *ex* W. J. M. Maassen collection (Fig. 116). Fig. 111: body of a male with pallial cavity open to show head and penis; Figs. 112, 116: shell; Fig. 113: outer face of operculum; Fig. 114: intestine and pallial organs of a male; Fig. 115: dorsal side (left) and ventral side (right) of penis. Scale bar = 1 mm.

valvataeformis Möllendorff, 1873, according to Radoman (1983).

Islamia valvataeformis (Möllendorff, 1873)

Hydrobia valvataeformis Möllendorff, 1873: 59.

Type Locality: ". . . an Steinen in der Quelle der Bosna, welche am Fuss des Igmangebirges bei Sarajevo . . .", Bosnia. According to Radoman (1983: 126) the type locality corresponds to "Vrelo Bosne, near Sarajevo".

Type Material: Möllendorff (1873) did not give any information about the type material.

Horatia servaini Bourguignat, 1887: 52.

Type Locality: "Sources de la Bosna, pres de Sérajewo, Bosnie".

Type Material: syntypes (2 shells) in the Bourguignat collection, Museum d'Historie Naturelle de Genève, Geneva, Switzerland (Binder, 1957).

Material Examined

–Vrelo Bosne, Sarajevo, Bosnia, 34T BP 85, G. Vigna & A. Vigna leg. (2 males, 3 shells).

Description

Shell very small, valvatiform, conical-ovoid, thin, pale whitish, waxen, transparent when fresh and clean; microsculpture of protoconch unknown; spire well raised, consisting of 3.5–4.25 rapidly growing convex whorls; last whorl large, dilated, more or less descending near aperture; umbilicus rather small; aperture prosocline, roundish to ovoid; peristome complete, thin, slightly thickened at columellar margin and slightly reflected at lower and columellar margin (Fig. 112; Bourguignat, 1887: 52, figs. 8, 9, as *Horatia servaini;* Radoman, 1973b: 227, 229, fig. 1A, as *Islamia* (*Islamia*) *servaini;* Radoman, 1983: 126, pl. 9, fig. 148). Dimensions: height = 1.62–2.00 mm; diameter = 1.53–1.81 mm (Radoman, 1983: Tab. 7).

Operculum thin, yellowish, paucispiral, without thickening or outgrowth at centre of inner face (Fig. 113; Radoman, 1973b: 227, as *Islamia* (*Islamia*) *servaini;* Radoman, 1983: 124).

Body pigmented; eye spots present (Fig. 111; Giusti et al., 1981: fig. 4.3, as *Islamia servaini*).

Male genitalia with penis large, elongated, dorso-ventrally flat, with cylindrical outline, apically bifid due to well-developed penial lobe on left side, slightly larger than tip of penis proper and containing mass of glandular cells; muscular pleat on ventral side of penis about 2/3 of penis length near base of penial lobe; penial duct zig-zagging through right portion of penis to open at tip of penis proper (Fig. 115; Radoman, 1973b: 227, 231, 233, fig. 3, as *Islamia* (*Islamia*) *servaini;* Giusti et al., 1981: fig. 4.3, as *Islamia servaini;* Radoman, 1983: 124, 126, fig. 69C).

Female genitalia with only two seminal receptacles arising rather close to one another from distal renal oviduct half way between end of loop (where proximal seminal receptacle arises in most hydrobiids having two seminal receptacles) and where oviduct enters albumen gland (near where distal seminal receptacle arises); that arising proximally (closer to end of loop) being rather well developed, always larger and longer than other, usually wider at apex than at base and with short but evident stalk; that arising distally (closer to where oviduct enters albumen gland) being very small and usually without evident stalk; bursa copulatrix absent; seminal groove running along ventral side of capsule gland (Radoman, 1973b: 227, fig. 2, as *Islamia* (*Islamia*) *servaini;* Radoman, 1973a: 6, 10; 1983: 40, 124, fig. 69A, B).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9–11 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 25–28 small denticles anteriorly; second marginal teeth scraper-shaped, with long and slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Radoman, 1973b: 227, fig. 2, as *Islamia* (*Islamia*) *servaini;* Giusti et al., 1981: 53, pl. 3, figs. 1–3, as *Islamia servaini;* Radoman, 1983: 124).

Stomach without posterior caecum; intestine with relatively undeveloped, U-like bend on pallial wall (Fig. 114; Radoman, 1973a: 6; Giusti et al., 1981: fig. 4.3, as *Islamia servaini;* Radoman, 1983: 40).

Osphradium variable in size, kidney-shaped; ctenidium consisting of 13–15 lamel-

lae (Fig. 114; Giusti et al., 1981: 53, fig. 4.3, as *Islamia servaini*).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1973b: 227, as *Islamia* (*Islamia*) *servaini;* Radoman, 1973a: 6; 1983: 124).

Taxonomy

Radoman (1973a: 10) established *Islamia* without a description or definition, but only by combining it with an available species group name and some new species. After 1930, this condition did not make a generic name available (ICZN, 1999: Art. 13.6). However, at the same time he designated a type species for the new nominal genus and introduced the new family group taxon, Islamiinae, of which he gave a diagnosis. Hence, we can consider this as a "combined description of a new family-group taxon and a new genus," which confers availability to each name (ICZN, 1999: Art. 13.5).

The genus *Islamia* is characterized by: shell very small, ovoid to planispiral; operculum without peg; penis with one glandular (rarely non-glandular) lobe; female genitalia with two seminal receptacles, proximal larger than distal, and without bursa copulatrix; central tooth with one or two pairs of basal cusps.

Adriolitorea Radoman, 1973b (p. 234; type species: *Islamia zermanica* Radoman, 1973a) and *Mienisiella* Schütt, 1991 (p. 134; type species: *Mienisiella mienisi* Schütt, 1991) are junior synonyms of *Islamia* Radoman, 1973a. *Adriolitorea* was introduced by Radoman (1973b) as a subgenus of *Islamia* and then regarded as synonym of the latter by Radoman (1983). *Mienisiella* is considered to be a junior synonym of *Islamia* on the basis of personal unpublished data. Schütt (1991) described the female genitalia of *M. mienisi* Schütt, 1991, and *M. gaillardoti* (Germain, 1911) as having a very small bursa copulatrix and one seminal receptacle. Study of topotypical specimens of *M. mienisi* and others of *M. gaillardoti* from many localities in Israel confirmed what is clearly evident from Schütt's (1991: fig. 5c): the two species have two seminal receptacles located and shaped exactly as in the *Islamia* species. Penis structure in *Mienisiella* (see Schütt 1991: 134–135, figs. 5b, 6b) is also exactly the same as that of the *Islamia* species. In fact, Schütt's second "small, simple excrescence on left side of penis" is the muscular pleat described above on the penis of *I. valvataeformis* and present on the penis of many *Islamia* species studied up to now. Study of *M. gaillardoti* also showed that the penial duct runs in the right side of the penis to open at the tip of the penis proper (right branch of bifid apex of penis) and not, as figured by Schütt (1991), at the tip of the penial lobe (left branch of bifid apex of penis).

Boeters (1998) mistakenly regarded *Islamia* as a junior synonym of *Neohoratia*. In fact, he did not base this conclusion on the concordance between the type species of *Neohoratia* and *Islamia* (*Valvata* (?) *subpiscinalis* Kuščer, 1932, and *Horatia servaini* Bourguignat, 1887 [a junior synonym of *Hydrobia valvataeformis* Möllendorff, 1873], respectively), but on the fact that an alleged "*Neohoratia*" species from western Europe actually turns out to be an *Islamia* species: *Islamia* cf. *minuta* (Draparnaud, 1805) (see "Descriptions of some taxa misidentified as *Hauffenia* species" below).

A number of species from different sites in Europe and Turkey have been assigned to Islamia by Giusti & Pezzoli (1980), Giusti et al. (1981), Reischütz (1988), Radoman (1973a, b, 1983) and Bodon et al. (1995a, b). Some of them, assigned to *Islamia* on the basis of shell characters, are in need of revision.

Karevia Hadžišče, 1959

Karevia Hadžišče, 1959: 81–82, as a subgenus of *Ohrigocea* Hadžišče, 1959.

Types Species: *Ohrigocea* (*Karevia*) *prlitchevi* Hadžišče, 1959, by subsequent designation (Radoman, 1963a) according to ICZN (1999: Art. 69.2.2). *Ohrigocea prlitchevi* is a junior synonym of *Karevia ornata* (Radoman, 1957), according to Radoman (1963a, b, 1983).

Karevia ornata (Radoman, 1957)

Pseudamnicola ornata Radoman, 1957: 88–89, figs. 3, 6, 7C, F, 8.

Type Locality: ". . . su uz istočnu obalu Ohridskog jezera, po obalskom kamenju, počev od izvora Veli Dab pa do početka peskovite, južne obale jezera, prema Sv. Naumu.", Lake Ohrid, Macedonia. The type locality is "Lake Ohrid, on the bank stones by Veli Dab. Spread from this locality to a great sandy beach near Sveti Naum", according to Radoman (1983: 81).

Type Material: lectotype (BEO 161, shell) at

the Prirodnjacki Muzej u Beograd, together with a paralectotype (BEO 162, shell) (Jovanović, 1991).

Ohrigocea (*Karevia*) *prlitchevi* Hadžišče, 1959: 83–86, figs. 20, 21.

Type Locality: ". . . lebt an seichten steinigen Zonen der Litoralregion auf der nordöstlichen, östlichen und sudöstlichen Seite des Sees [Lake Ohrid], Macedonia".

Type Material: Hadžišče (1959) did not give any information about the type material.

Material Examined

—Harbour of Trpezjca, Lake Ohrid, Macedonia, 34T DL 83, 5.1976, *ex* W. J. M. Maassen collection (1 shell with dried soft parts).

Description

Shell very small, valvatiform-planispiral, adorned with two rows of more or less raised nail-like projections, regularly spaced to follow course of a peripheral keel and basal keel; surface of protoconch malleated; spire depressed, consisting of 2.75–3.25 rather rapidly growing whorls; last whorl dilated, descending slightly near aperture, its external wall with peripheral keel and its lower wall with basal keel; umbilicus very wide; aperture prosocline, irregularly rhomboidal, angled above and at two keels; peristome complete, thin, slightly reflected only at columellar margin (Fig. 116; Radoman, 1957: 88–89, fig. 3; Hadžišče, 1959: 83–86, figs. 20, 21, as *Ohrigocea* (*Karevia*) *prlitchevi;* Hadžišče, 1959: 86–87, fig. 23, as *Ohrigocea* (*Karevia*) *sandanskii;* Maassen, 1980: pl. 17, figs. 35, 36; Radoman, 1963a: 78–79, fig. 7, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1963b: 95–96, fig. 7, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1983: 80–81, pl. 5, fig. 77, as *Dolapia ornata;* Jovanović, 1991: pl. 5, fig. 40, as *Dolapia ornata*). Dimensions: height = 0.72–1.10 mm; diameter = 1.45–1.73 mm (Radoman, 1983: tab. 5).

Operculum yellowish red, paucispiral, probably without peg though not specified.

Body pigmented; eye spots present.

Male genitalia with penis large, flat with apex rather pointed and lobe on left side about 2/3 of penis length (Radoman, 1957: 89, fig. 7F; Hadžišče, 1959: 86, fig. 20, as *Ohrigocea* (*Karevia*) *prlitchevi;* Hadžišče, 1959: 87, fig. 24, as *Ohrigocea* (*Karevia*) *sandanskii;* Radoman, 1963a: fig. 15, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1963b: fig. 15, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1983: 80, fig. 41, as *Dolapia ornata*).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle much larger than distal, which is rudimentary; bursa copulatrix large, arched, kidney- or crescent-shaped, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1957: 89, fig. 7C; Radoman, 1963a: 78, fig. 15, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1963b: 95, fig. 15, as *Pseudamnicola* (*Karevia*) *ornata;* Radoman, 1973a: 6, as *Dolapia ornata;* Radoman, 1983: 40, 80, fig. 41, as *Dolapia ornata*).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 4–5 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9–13 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 14–20 denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Radoman, 1957: 90, fig. 6; Hadžišče, 1959: 85–86, fig. 22, as *Ohrigocea* (*Karevia*) *prlitchevi;* Hadžišče, 1959: 86–87, fig. 24, as *Ohrigocea* (*Karevia*) *sandanskii*).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6, as *Dolapia ornata;* Radoman, 1983: 40, as *Dolapia ornata*).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1957: 91, fig. 8; Radoman, 1973a: 6, as *Dolapia ornata;* Radoman, 1983: 80, as *Dolapia ornata*).

Taxonomy

Karevia is here considered a distinct genus, but its relationships to *Ohridohauffenia* Hadžišče, 1959, and *Ohrigocea* Hadžišče, 1959, need to be clarified. *Karevia* is characterized by: shell very small, valvatiform-

planispiral, bicarinate and adorned with two rows of nail-like projections; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal larger than distal, which is rudimentary, and large, crescent-shaped bursa copulatrix with anterior duct; central tooth with one pair of basal cusps. It includes only the type species, which is endemic to Lake Ohrid.

Dolapia Radoman, 1983 (p. 80, type species: *Pseudamnicola ornata,* Radoman, 1957), is a junior synonym of *Karevia* Hadžišče, 1959. In fact, apparently overlooking his previous designation of *Ohrigocea* (*Karevia*) *prlitchevi* Hadžišče, 1959 (as *P. ornata,* with *O. prlitchevi* as a junior synonym), as type species of *Karevia,* Radoman (1973a) designated another type species: *Ohrigocea* (*Karevia*) *miladinovorum* Hadžišče, 1959. At the same time, he introduced a new genus, *Dolapia,* for *P. ornata.* However, he (Radoman, 1973a: 8) established this nominal genus without a description or definition but only by combining it with an available species group name. After 1930, this condition does not make a generic name available (ICZN, 1999: Art. 13.6).

Ohrigocea (*Karevia*) *sandanskii* Hadžišče, 1959 (pp. 86–87, figs. 23, 24; type locality: ". . . lebt auf der östlichen und sudöstlichen Seite des Sees, in den seichten Teilen seines steinigen Litorals [Lake Ohrid]", Macedonia figs. 117–122 is another junior synonym of *Karevia ornata* (Radoman, 1963a, b, 1983).

Kerkia Radoman, 1978

Kerkia Radoman, 1978: 29.
Type Species: *Hauffenia kusceri* Bole, 1961, by original designation.

Kerkia kusceri (Bole, 1961)

Hauffenia kusceri Bole, 1961: 62, 67, fig. 3A.
Type Locality: "Krška jama", Slovenia. According to Radoman (1983: 112), the type locality is "Jama Krke (cave), southeast of Ljubljana".
Type Material: Bole (1961) did not give any information about the type material.

Material Examined

–Spring of the Krka River, Krka, Slovenia, 33T VL 88, M. Bodon leg. 16.6.1985 (1 male, 1 female, many shells).

–"Krška Jama" cave, S. 74, Krka, Slovenia, 33T VL 88, F. Gasparo & F. Stoch leg. 26.9.1992 (13 specimens, 2 shells).

Description

Shell very small, valvatiform, thin, whitish; surface of protoconch malleated; spire depressed to slightly raised, consisting of 2.75–3.25 rather rapidly growing convex whorls; last whorl dilated, more or less descending near aperture; umbilicus wide; aperture prosocline, roundish to oval; peristome complete, thin, slightly reflected at columellar margin. (Figs. 89, 117; Bole, 1961: 62, 67, fig. 3A; Radoman, 1978: 29–30, pl. 4, figs. 3, 4; 1983: 110, 112, pl. 8, fig. 128). Dimensions: height = 0.97–1.44 mm; diameter = 1.60–2.34 mm (Radoman, 1983: tab. 6).

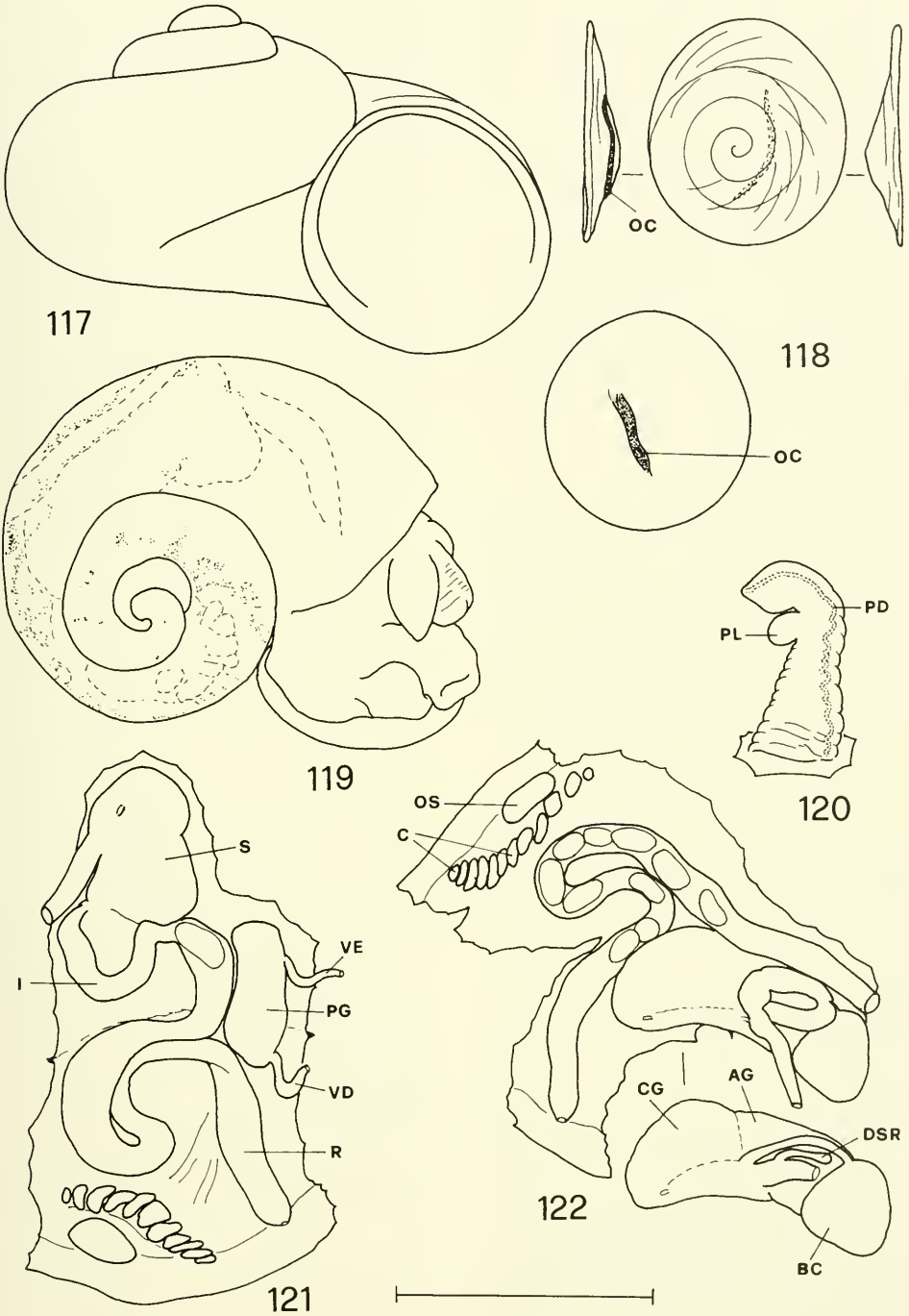
Operculum slightly thickened, paucispiral, with low crest-like thickening at centre of inner face (Figs. 38, 39, 118; Bole, 1961: 62, 67, fig. 3A; Radoman, 1978: 30; 1983: 112; Bole, 1993: 10, fig. 2B).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent (Fig. 119).

Male genitalia with prostate gland bulging well into pallial cavity; penis elongated, cylindro-conical, flat, slightly dilated then tapering near apex, with large non-glandular lobe on left side about 2/3 of penis length; penial duct zig-zagging through right portion of penis to open at penis tip (Figs. 120, 121; Bole, 1961: 62, fig. 3A; Radoman, 1978: 29, fig. 2C; 1983: 110, fig. 58C; Bole, 1993: 10, fig. 1C).

Female genitalia with distal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle very long, slender; bursa copulatrix very large, oval to subtriangular, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Fig. 122; Radoman, 1978: 29, fig. 2A, B; 1983: 40, 110, fig. 58A, B). Bole (1993, fig. 1B), illustrates female genitalia with a very small bursa copulatrix; this is due to a misidentification of a female of the *Hauffenia* species living in the same aquifer.

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; two basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 8–9 denti-



FIGS. 117–122. Shell, operculum and anatomical details of *Kerkia kusceri* (Bole, 1961) from the spring of the Krka River, Krka, Slovenia, M. Bodon leg. 16.6.1985. Fig. 117: shell; Fig. 118: outer face (top centre), profile (top left and right) and inner face (below) of operculum; Fig. 119: body; Fig. 120: dorsal side of penis; Fig. 121: prostate gland, stomach, intestine and pallial organs of a male; Fig. 122: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

cles, central of which longer and larger; first marginal teeth with apical row of 12–16 denticles; second marginal teeth with rather long row of 14–18 denticles (Bole, 1961: 62, 67, fig. 3A; 1993: 10, fig. 2A).

Stomach without posterior caecum; intestine with well developed, S-like bend on pallial wall (Figs. 121, 122; 1978: 29, fig. 2D; Radoman, 1983: 40, fig. 58D).

Osphradium variable in size, ovoid or elongated; ctenidium consisting of about 11–12 lamellae (Figs. 121, 122; Bole, 1961: 62, 67; 1993: fig. 1A).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1978: 29; 1983: 110).

Taxonomy

The genus *Kerkia* is characterized by: shell very small, valvatiform to planispiral; operculum without peg, but with crest-like projection or thickening on inner face; penis with one simple lobe; female genitalia with distal seminal receptacle and very large, oval to subtriangular, bursa copulatrix with anterior duct; central tooth with two pairs of basal cusps. It includes the type species and a recently described species: *K. brezicensis* Bodon & Cianfanelli, 1996, both from Slovenia. *Kerkia brezicensis* differs from *K. kusceri* in shell (flat spire), opercular (circular thickening on inner face), and anatomical (slender penial apex, smaller penial lobe) characters (Bodon & Cianfanelli, 1996).

Lobaunia Haase, 1993

Lobaunia Haase, 1993: 98–99.

Type Species: *Lobaunia danubialis* Haase, 1993, by original designation.

Lobaunia danubialis Haase, 1993

Lobaunia danubialis Haase, 1993: 99–105, figs. 8B, 9–15.

Type Locality: "Peilrohr A 63 am Eberschüttwasser im SE Wiens", Austria.

Type Material: holotype (NHMW 85027, female) at the Naturhistorisches Museum Wien, Vienna, Austria; paratypes at the Naturhistorisches Museum Wien (NHMW 85028, 1 male: NHMW 85884, 31 shells) and in the Stojaspal collection (3230, 16 shells), Vienna, Austria (Haase, 1993).

Material Examined

– Pipe A89, Lobau, Wien, Austria, Pospisil leg. 24.1.1992, *ex* M. Haase collection (1 shell with dried soft parts, 8 shells).

Description

Shell very small, valvatiform-planispiral, thin, whitish, transparent when fresh; surface of protoconch malleated; spire almost flat, consisting of 2.25–2.75 rather rapidly growing convex whorls; last whorl dilated, descending slightly near aperture; umbilicus wide; aperture prosocline, oval; peristome complete, thin, slightly reflected only at columellar margin (Fig. 123; Haase, 1993: 98–99, 104–105, fig. 9A-C; Boeters, 1998: 29, figs. H13–14). Dimensions: height = 0.50–0.84 mm; diameter = 0.86–1.31 mm (Haase, 1993: table 1).

Operculum thin, yellow-orange, paucispiral, slightly thickened at centre, but without outgrowth on inner face (Fig. 124; Haase, 1993: 98–99, figs. 10A, B).

Body unpigmented (a few black spots on visceral sac level with stomach); eye spots absent (Haase, 1993: 98).

Male genitalia with penis rather short, flat, tapering slightly near apex and ending in rather obtuse tip; penial duct zig-zagging through central portion of penis to open at penis tip; terminal portion of penial duct (immediately before opening) with very small stylet (Haase, 1993: 99, 103, Figs. 8B, 15; Boeters, 1998: 29, fig. H15).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle small but proportionally rather developed, arising from oviduct at end of loop; bursa copulatrix small, slightly larger than seminal receptacle, with very short duct entering on anterior side; according to Haase (1993), the seminal groove ("Ventralkanal") is a distinct duct – possibly similar to the "spermathecal duct" described by Davis et al. (1982) in *Spurwinkia salsa* (Pilsbry, 1895) – completely separated from the lumen of the capsule gland, starting from proximal part of capsule gland and ending in the gonopore; the renal oviduct is supposed to end by entering the albumen gland through an opening ("Offnung für Eizellen"); spermatozoa are supposed to enter the gonopore, to run in the "spermathecal duct", then enter the pallial oviduct and, finally, to reach renal oviduct (and hence seminal receptacle) through another opening ("Offnung für Sper-

matozoen") connecting albumen gland directly to renal oviduct (Haase, 1993: 98–99, 102, 104, figs. 8B, 12–14; Boeters, 1998: 29, fig. H16).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long and robust central denticle and 5 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–11 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 17–21 small denticles anteriorly; second marginal teeth scraper-shaped, with long and slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 13–15 small denticles (Haase, 1993: 98–99, figs. 11A, B).

Stomach without posterior caecum; intestine with well developed, S-like bend on pallial wall (Haase, 1993: 98–99, fig. 12).

Osphradium unknown; ctenidium consisting of 8–9 lamellae (Haase, 1993: 99).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Haase, 1993: 99).

Taxonomy

Lobaunia is here considered a junior synonym of *Hauffenia* Pollonera, 1898 (see "Status and relationship of Hauffenia"). Haase (1993) described *Lobaunia* as a distinct genus based on the extremely peculiar structure of the female genitalia (see description) reconstructed by serial sectioning. If these characters were true, this genus would be distinct from all other European hydrobiids (valvatiform and non-valvatiform). However, the fact that *Lobaunia* matches *Hauffenia, Neohoratia* Schütt, 1961, *Vrania* Radoman, 1978, and *Erythropomatiana* Radoman, 1978, in male genital characters and also lives in an area where *Hauffenia* is widespread, invited prudence and suggested the need for more careful anatomical study. Asked for details of the anatomy of *Lobaunia,* Haase (personal communication, 3.2.1995) replied that he had new data suggesting that his reconstruction of the female genitalia of *Lobaunia,* based on only one specimen, might be incorrect and that *Lobaunia* might correspond to *Hauffenia.*

Lobaunia included only the type species from Austria.

Lyhnidia Hadžišče, 1959

Lyhnidia Hadžišče, 1959: 88.

Type Species: *Lyhnidia hadzii* Hadžišče, 1959, by subsequent designation (Radoman, 1963a).

Lyhnidia hadzii Hadžišče, 1959

Lyhnidia hadzii Hadžišče, 1959: 90–93, figs. 27–29.

Type Locality: ". . . lebt in den seichten Teilen des steinigen Litorals auf der östlichen und südöstlichen Seite des Sees [Lake Ohrid] wie auch in seinem Sublitoral, nämlich der Schalenzone und besonders der Zone der lebenden Dreissensien, Macedonia". According to Radoman (1983: 116) the type locality is "Lake Ohrid, by Veli Dab".

Type Material: Hadžišče (1959) did not give any information about the type material.

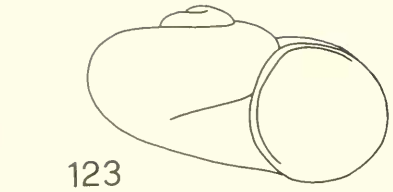
Material Examined

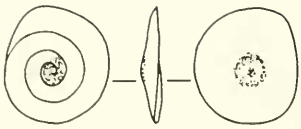
– Harbour of Trpezjca, Lake Ohrid, Macedonia, 34T DL 83, 5.1976, *ex* W. J. M. Maassen collection (2 shells with dried soft parts).

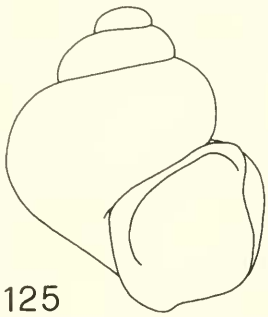
Description

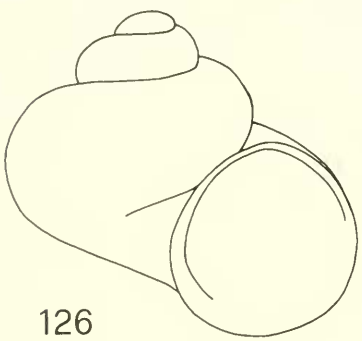
Shell very small, valvatiform-globose conical, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire rather raised, conical, consisting of 3.25–3.5 rather rapidly growing convex whorls; last whorl large, slightly dilated, slightly descending near aperture; umbilicus very small, slit-like; aperture prosocline, irregularly square; peristome complete, sinuous, with external margin concave above, convex at centre, concave again at border with the lower margin, lower margin convex and slightly reflexed at border with columellar margin, columellar margin rather vertical, little thickened and reflexed (Fig. 125; Hadžišče, 1959: 90–91, figs. 27–28; Radoman, 1963a: 77, fig. 5a; 1963b: 93, fig. 5a; 1983: 115–116, table 7, pl. 8, fig. 135). Dimensions: height = 0.92–1.15 mm; diameter = 0.84–1.08 mm, according to Radoman, 1983: table 7 (height = 1.0–1.2 mm; diameter = 0.9–1.1 mm, according to Hadžišče, 1959).

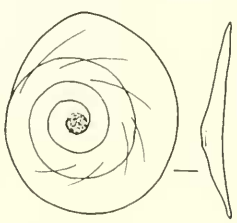
Operculum thick, yellowish red, paucispiral,

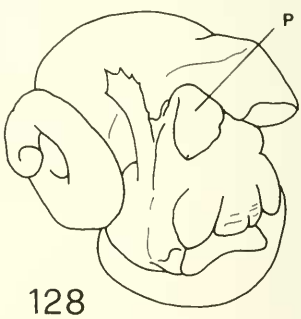


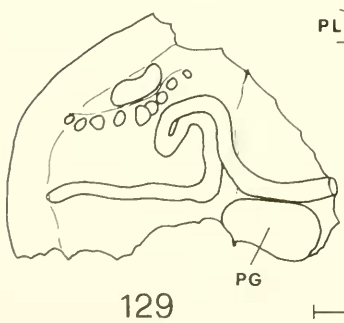


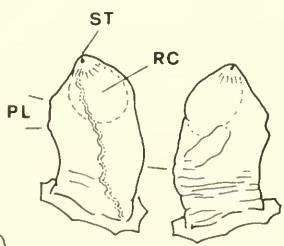


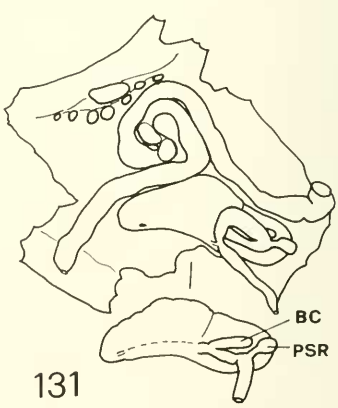












FIGS. 123–131. Shell and operculum of *Hauffenia danubialis* (Haase, 1993), from the pipe A89, Lobau, Wien, Austria, Pospisil leg. 24.1.1992, *ex* M. Haase collection (Figs. 123, 124), shell of *Lyhnidia hadzii* Hadžišče, 1959, from the harbour of Trpezjca, Lake Ohrid, Macedonia, 5.1976, ex W. J. M. Maassen collection (Fig. 125) and shell, operculum and anatomical details of *Erythropomatiana verdica* Radoman, 1978, junior synonym of *Hauffenia subpiscinalis* (Kuščer, 1932), from spring on right bank of the Verd brook, near the Verd spring, Vrhnika, Slovenia, M. Bodon leg. 17.6.1985 (Figs. 126–131). Figs. 123, 125, 126: shell; Figs. 124, 127: outer face (left), profile (Fig. 124 centre; Fig. 127 right) and inner face (Fig. 124 right) of operculum; Fig. 128: body of a male with pallial cavity open to show head and penis; Fig. 129: intestine and pallial organs of a male; Fig. 130: dorsal side (left) and ventral side (right) of penis; Fig. 131: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

without outgrowth at centre of inner face (Hadžišče, 1959: 92).

Body pigmented; eye spots present.

Male genitalia with penis elongated, flat, tapering near apex, ending in rather pointed tip and with a small lobe on left side near apex (Hadžišče, 1959: 92, fig. 28; Radoman, 1963a: 77, fig. 13a; 1963b: 93, fig. 13a; 1983: 116). Hadžišče (1959, fig. 29) and Radoman (1963a: fig. 13a; 1963b: fig. 13a) show a distinct penial lobe; however, Radoman's (1983: 116) diagnosis of the genus does not mention this character: "Penis . . . smooth (without any outgrowth)"; the diagnosis is based, rather, on *L. gjorgjevici,* which has a penial tip without a distinct lobe.

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle rather well developed; bursa copulatrix large, kidney-shaped, with rather short, wide duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1963a: 77, fig. 13a; 1963b: 93, fig. 13a; 1973a: 6, 10; 1983: 40, 114, 116). Radoman's diagnosis (1983: 116) described a bursa copulatrix "very small, hardly visible behind the oviduct loop, with a long duct (fig. 63)", but it was based on *L. gjorgjevici,* not on *L. hadzii.*

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 4 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with about 8–9 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of about 23 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Hadžišče, 1959: 92, fig. 29; Radoman, 1963a, fig. 17b; 1963b, fig. 17b; 1983: 114).

Stomach without posterior caecum; intestine unknown (Radoman, 1963a, fig. 13a; 1963b, fig. 13a; 1973a: 6; 1983: 40, 116).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and slightly shorter pleuro-suboesophageal connectives (Radoman, 1973a: 6; 1983: 116).

Taxonomy

Lyhnidia is here considered a distinct genus. However, some of its anatomical details are unknown, and its relationships to other Balkan genera require further study. *Lyhnidia* is characterized by: shell very small, valvatiform-globose conical; operculum without peg; penis with one simple lobe; female genitalia with proximal seminal receptacle and large, kidney-shaped bursa copulatrix with anterior duct; central tooth with one pair of basal cusps.

Apparently overlooking his earlier type designation (as in the case of *Karevia*), Radoman (1967) erroneously reported *Lyhnidia gjorgjevici* Hadžišče, 1959, as a type species of *Lyhnidia.*

Radoman (1983) included four other species from Lake Ohrid in *Lyhnidia: L. gjorgjevici* Hadžišče, 1959, *L. karamani* Hadžišče, 1959, *L. stankovici* Hadžišče, 1959, *L. sublitoralis* Radoman, 1967, distinguished on the basis of few shell characters.

Neohoratia Schütt, 1961a

Neohoratia Schütt, 1961a: 71–72, as subgenus of *Horatia.*

Type Species: *Valvata* (?) *subpiscinalis* Kuščer, 1932, by original designation.

Neohoratia subpiscinalis (Kuščer, 1932)

Valvata (?) *subpiscinalis* Kuščer, 1932: 51–53, pl. 5, fig. 1.

Type Locality: "Der Rak-Bach unweit der jugoslavisch-italienischen Grenze", Slovenia.

Type Material: holotype (2001a) in the Kuščer collection, Ljubljana, Slovenia (Kuščer, 1932).

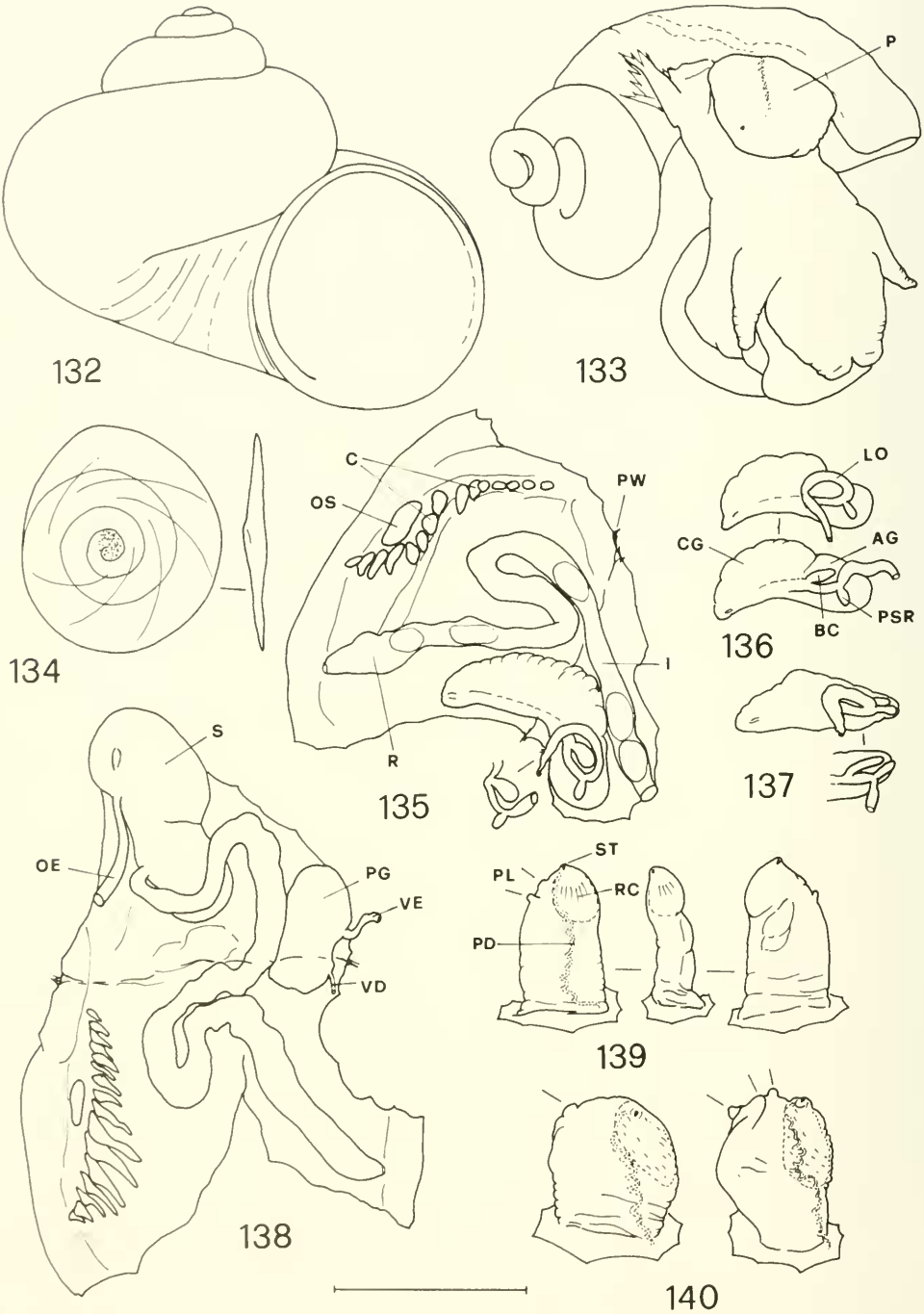
Erythropomatiana verdica Radoman, 1978: 36, pl. 5, figs. 20, 21.

Type Locality: "Quelle im Bett des Flüsschens neben dem Dorf Verd, unweit von Vrhnika", Slovenia.

Type Material: holotype and two paratypes (SMF 249615) are at the Senckenberg-Museum, Frankfurt am Main, Germany (Jovanović, 1991).

Material Examined

Bole (1967a) studied the anatomy of specimens from the subterranean waters of the Ljubljanica basin, Slovenia. The specimens



FIGS. 132–140. Shell, operculum and anatomical details of *Hauffenia subpiscinalis* (Kuščer, 1932) from the "Želške Jame" caves, S. 576, near Rakek (Slovenia), 3.3.1966, *ex* F. Velkovrh collection (Figs. 132–136, 138, 140) and from the spring Obrh, Gorenje Jezero, Cerknica, Slovenia, M. Bodon leg. 19.6.1985 (Figs. 137–139). Fig. 132: shell; Fig. 133: body of a male with pallial cavity open to show head and penis; Fig. 134: outer face (left) and profile (right) of operculum; Fig. 135: renal and pallial oviduct, intestine and pallial organs of a female; Figs. 136–137: renal and pallial oviduct of two females; Fig. 138: prostate gland, stomach, intestine and pallial organs of a male; Fig. 139: dorsal (left), right (centre) and ventral side (right) of penis; Fig. 140: dorsal side of penis of two males. Scale bar = 1 mm.

examined for the present study were from the following sites (the first two sites were at the spring and caves which feed the Rak River, so they belong to the type locality):

- "Želške Jame" caves, S. 576, near Rakek, Slovenia, 33T VL 46, 3.3.1966, *ex* F. Velkovrh collection (2 males, 1 female); M. Buda Dancevich & F. Stoch leg. 1.7.1993 (2 shells).
- Kotla spring, Rakov Škocjan. Plentiful karstic spring flooding into the Rak River, Slovenia, 33T VL 46, M. Bodon leg. 18.6.1985 (1 female, many shells); M. Buda Dancevich & F. Stoch leg. 1.7.1993 (many shells).
- Obrh spring, Gorenje Jezero, Cerknica. Plentiful karstic spring in the Cerkniško lake basin (the lake water floods into sinkholes and feeds the Rak River), Slovenia, 33T VL 56, M. Bodon leg. 19.6.1985 (2 males, 1 female, 15 shells).
- Spring of Žerovniščica, Žerovnica, Cerknica, Slovenia, 33T VL 57, F. Gasparo & F. Stoch leg. 14.10.1994 (1 male).
- "Planinška Jama" cave, S. 748, Planina, Slovenia, 33T VL 47, F. Gasparo & F. Stoch leg. 5.6.1993 (1 male, 4 shells).
- Močilnik springs, Vrhnika; plentiful karstic springs which feed the Ljubljanica River, Slovenia, 33T VL 49, M. Bodon leg. 17.6.1885 (2 females, many shells).
- Spring on right bank of Verd brook, near the Verd spring, Vrhnika, Slovenia, 33T VL 49, M. Bodon leg. 17.6.1985 (2 males, 1 female, many shells) (type locality of *Erythropomatiana verdica*).
- Ukovnik cave, S. 1165, Spodnja Idrija, Idrijca valley, Slovenia, 33T VM 20, F. Gasparo & F. Stoch leg. 5.6.1993 (1 female).
- "Draga pri Ponikvah" cave, S. 972, Ponikve, Štanjel, Slovenia, 33T VL 17, S. Dolce & F. Stoch leg. 19.7.1994 (1 male, 1 shell).
- Springs of the Timavo River, S. Giovanni al Timavo, Duino-Aurisina, Trieste, Friuli-Venetia Julia, Italy, 33T UL 9071, M. Bodon leg. 31.3.1991 (1 female, many shells) (Pezzoli, 1988a, cited as *Islamia* (?) sp.).
- Cave of Trebiciano, no. 17 VG, Trieste, Friuli-Venetia Julia, Italy, 33T VL 0959, S. Dolce & F. Stoch leg. 8.12.1991 (1 juv. specimen, 4 shells), 26.1.1992 (2 males, 1 female, 2 spec. and 7 juv. spec.), F. Stoch leg. 2.7.1996 (10 shells).
- Spring in the square of Bagnoli della Rosandra which feeds a basin, Trieste, Friuli-Venetia Julia, Italy, 33T VL 1151, M. Bodon, M. M. Giovannelli & F. Stoch leg. 29.3.1991 (2 juv. spec., many shells).

For other localities in Italy where only conchological material has been found see Pezzoli (1988a) and Bodon & Giovannelli (1993). For other localities in Slovenia, see Kuščer (1932), Bole (1970, 1979, 1985) and Bole & Slapnik (1997).

Description

Shell very small, valvatiform, thin, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire generally well raised, consisting of 3.25–3.75 rapidly growing, convex whorls; last whorl dilated, more or less descending, often slightly detached near aperture; umbilicus rather narrow; aperture wide, prosocline, roundish; peristome complete, thin, slightly reflected only at columellar margin (Figs. 90, 126, 132; Kuščer, 1932: 51–52, pl. 5, fig. 1; Schütt, 1961a: 71; Bole, 1970: 92, fig. 3A–G; Bole: 1979a, fig. 1(5a–5b); Maassen: 1975, pl. 27, figs. 1–3; Bole & Velkovrh, 1986: fig. 31; Hershler & Longley, 1986: fig. 7I). Dimensions: height = 1.3–2.6 mm; diameter = 1.4–2.9 mm.

Operculum thin, yellowish, paucispiral, slightly thickened, but lacking peg or any kind of outgrowth at centre of inner face (Figs. 41, 127, 134; Bole, 1967a: 84, fig. 3A5; 1993: 8, fig. 2B).

Body unpigmented (sometimes a few traces of pigment in wall of visceral sac); eye spots absent (Figs. 128, 133).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather short, flat, with apex enlarged, blunt or slightly pointed; 1–3 small, knob-like lateral lobes on left side near apex; sometimes slightly raised pleat at centre of ventral side about 2/3 of penis length; penial duct zig-zagging through central portion of penis to open at penis tip; large, pyriform mass of refringent cells inside penis apex to right of penial duct; terminal part of penial duct (immediately before opening) with very small stylet (Figs. 100, 129–130, 138–140; Bole, 1967a: 84, fig. 3A4; 1993: 8, fig. 1C).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle small, sessile or with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, small, but longer than seminal re-

ceptacle, not dilated at apex, arising very close to point at which oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Figs. 102, 103, 131, 135–137; Bole, 1967a: 84, fig. 3A3; 1993: 8, fig. 1B). Histological study of female genitalia gave results in line with those described for *H. tellinii*.

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; 2–3 basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9–13 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 19–25 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 10–12 very small denticles (Figs. 50–52; Bole, 1967a: 83, fig. 3A6; Hershler & Longley, 1986: fig. 28D; Bole, 1993: 8, fig. 2A).

Stomach without posterior caecum; intestine with well developed, S-like bend on pallial wall (Figs. 129, 131, 135, 139; Bole, 1967a: 83).

Osphradium variable in size, elongated, oval or kidney-shaped; ctenidium consisting of 9–16 lamellae (Figs. 129, 131, 135, 139; Bole, 1967a: 83, fig. 3A1; 1993: 8, fig. 1A).

Nervous system with very short connectives (Bole, 1967a: 84).

Taxonomy

Neohoratia is here considered a junior synonym of *Hauffenia* Pollonera, 1898 (see "The status and relationships of Hauffenia"). Schütt (1961a) introduced *Neohoratia*, as subgenus of *Horatia*, for *Valvata subpiscinalis* Kuščer, 1932. Subsequently, *Neohoratia* was regarded as a subgenus of *Hauffenia* by Boeters (1974), completely overlooked by Radoman (1978, 1983), and ranked as a full genus by Bole & Velkovrh (1986), Boeters (1988, 1998) and Bole (1993).

Erythropomatiana verdica Radoman, 1978, is here recognized as junior synonym of *Neohoratia subpiscinalis* (see taxonomic remarks to *H. subpiscinalis*, in the section on *Hauffenia* species).

Many nominal species from different south European localities (from Greece to Spain) have been assigned to *Neohoratia* (sometimes regarded as a subgenus of *Hauffenia* or *Horatia,* sometimes as a distinct genus) by Schütt (1962, 1980), Bernasconi (1975), Boeters (1981, 1988, 1998), Gittenberger (1982), Vidal-Abarca & Suarez (1985), Boeters & Rolan (1988), Bech (1990), Hinz et al. (1994), Ramos et al. (1992) and Rolan (1997a, b). All were assigned to Neohoratia on the basis of shell characters, only in few cases followed by anatomical study. All are in need of revision (see below).

Ohridohauffenia Hadžišče 1959

Ohridohauffenia Hadžišče, 1959: 74, as subgenus of *Ohridohoratia*.

Type Species: *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici* Hadžišče, 1959, by monotypy. *Ohridohoratia gjorgjevici* is a junior synonym of *Pseudamnicola depressa* Radoman, 1957, according to Radoman (1963a, b, 1983).

Ohridohauffenia depressa (Radoman, 1957)

Pseudamnicola depressa Radoman, 1957: 88–91, figs. 2, 5, 7B, E.

Type Locality: ". . . su uz istočnu obalu Ohridskog jezera, po obalskom kamenju, počev od izvora Veli Dab pa do početka peskovite južne obale jezera, prema Sv. Naumi", Lake Ohrid, Macedonia. According to Radoman (1983: 75) the type locality is "Lake Ohrid, on the bank stones by Veli Dab".

Type Material: lectotype (BEO 142, shell) is at Prirodnjacki Muzej u Beograd (Jovanović, 1991).

Ohridohoratia (*Ohridohauffenia*) *gjorgjevici* Hadžišče, 1959: 75–76, figs. 12, 13.

Type Locality: ". . . die ich an seichten Stellen des steinigen Litorals gefunden habe . . .", Lake Ohrid, Macedonia.

Type Material: Hadžišče (1959) did not give any information about the type material.

Description

Shell very small, valvatiform, depressed; microsculpture of protoconch unknown; spire rather depressed, consisting of 3–3.25 rapidly growing, slightly convex whorls; last whorl large, rather dilated, with distinct keel at periphery; umbilicus moderately wide; aperture prosocline, pyriform, distinctly angled at centre of external margin, with external margin

slightly concave immediately above and below keel; peristome complete, thin, slightly reflected only at columellar margin (Radoman, 1957: 88, fig. 2; Hadžišče, 1959: 75–76, fig. 12, as *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici;* Radoman, 1963a: fig. 4a; 1963b: fig. 4a; 1983: 75, pl. 5, fig. 69; Jovanović, 1991: pl. 5, fig. 35). Dimensions: height = 0.81–1.04 mm; diameter = 1.25–1.53 mm (Radoman, 1983: 75, table 5).

Operculum thin, yellowish red, paucispiral, slightly thickened, without outgrowth on inner face (Hadžišče, 1959: 76, as *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici;* Radoman, 1983: 75).

Body pigmented; eye spots present.

Male genitalia with penis large, flat with long conical tip, slightly obtuse apex, and one, more or less evident, sometimes pointed lobe on left side about 2/3 of penis length (Radoman, 1957: 91, fig. 7E; Hadžišče, 1959: 76, fig. 12, as *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici;* Radoman, 1963: fig. 12a; 1963b: fig. 12a; 1983: 75, fig. 37).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle much larger than distal, which is rudimentary; bursa copulatrix large, kidney-shaped, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1957: 90–91, fig. 7B; 1963a: fig. 12a; 1963b: fig. 12a; 1973a: 6; 1983: 75: fig. 37).

Radula with central tooth trapezoidal, its cutting edge with 9–11 denticles, central longer; long lateral wings and basal tongue; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 8–11 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 14–21 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of numerous, very small denticles (Radoman, 1957: 90, fig. 5; Hadžišče, 1959: 76, fig. 13, as *Ohridohoratia* (*Ohridohauffenia*) *gjorgjevici*).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and slightly shorter pleuro-suboesophageal connectives (Radoman, 1973a: 6; 1983: 75).

Taxonomy

Ohridohauffenia is here considered a distinct genus, but its relationships to *Ohrigocea* Hadžišče, 1959, and possibly also *Karevia* Hadžišče, 1959, need to be clarified. *Ohridohauffenia* is characterized by: shell very small, valvatiform, sometimes carinate; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal larger than distal (which is rudimentary), and large, kidney-shaped bursa copulatrix with anterior duct; central tooth with one pair of basal cusps.

Rotondia Radoman, 1964 (pp. 108, 109; type species: *Pseudamnicola* (*Rotondia*) *rotonda* Radoman, 1964, by original designation), is regarded as a junior synonym of *Ohridohauffenia* Hadžišče, 1959, by Radoman (1983). *Rotondia* was established without a description or definition, but only by combining it with some available nominal species; it is therefore not available (ICZN, 1999: Art. 13.6). Likewise, *Naumia* Radoman, 1973a, regarded by Radoman (1983) as a junior synonym of *Ohridohauffenia,* is not available. In fact, it was established by Radoman (1973a: 8, for *Pseudamnicola* (*Rotondia*) *st. naumi* [*sic*] Radoman, 1964) without a description or definition, but only by combining it with an available species group name. After 1930, this condition does not make a generic name available (ICZN, 1999: Art. 13.6).

Radoman (1983) includes five other species from Lake Ohrid and nearby springs in *Ohridohauffenia: O. sublitoralis* (Radoman, 1963a), *O. rotonda* (Radoman, 1964), *O. minuta* (Radoman, 1955), *O. drimica* (Radoman, 1964), and *O. sanctinaumi* (Radoman, 1964).

Ohrigocea Hadžišče, 1959

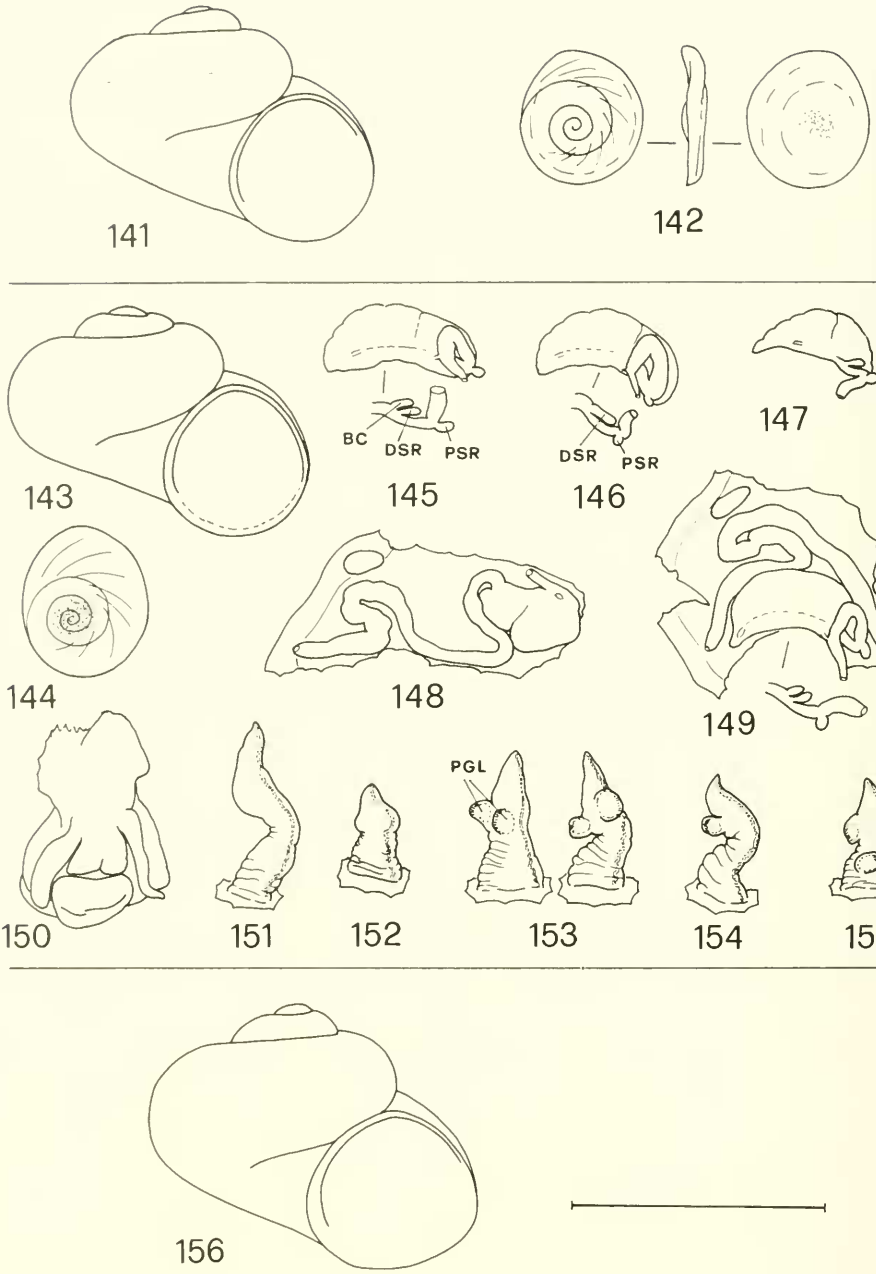
Ohrigocea Hadžišče, 1959: 76–77.

Type Species: *Ohrigocea samuili* Hadžišče, 1959, by subsequent designation (Radoman, 1963a).

Ohrigocea samuili Hadžišče, 1959

Ohrigocea (*Ohrigocea*) *samuili* Hadžišče, 1959: 77–79, figs. 14, 15.

Type Locality: "lebt in den seichten Zonen des steinigen Litorals auf der nord-östlichen, östlichen und sud-östlichen Seite des



FIGS. 141–156. Shell and operculum of *Ohrigocea samuili* Hadžišče, 1959, from H. Gorica, Lake Ohrid, Macedonia, 5.1975, *ex* W. J. M. Maassen collection (Figs. 141, 142); shell, operculum and anatomical details of *Pezzolia radapalladis* Bodon & Giusti, 1986, from the spring inside the Rio di Tonnego, Ponte della Vittoria, Rapallo, Genova, Liguria, Italy, M. Bodon leg. 16.5.1981, 4.10.1981, 6.11.1982 (Figs. 143, 144, 148–151) and from the spring on the right bank of the Bana Stream, below the tank of the aqueduct of Bana, Camogli, Genova, Liguria, Italy, M. Bodon leg. 26.1.1992 (Figs. 147, 152); anatomical details of Pezzolia sp. 2 from alluvial spring on bed of the Canate Stream near the cave of Cavassola, Genova, Liguria, Italy, 32T NQ 0222, M. Bodon leg. 24.12.1983 (Figs. 145, 155) and of *Pezzolia* sp. 1 from springs in the Nervi Stream valley, Genova, Liguria, Italy, 32T NQ 0315, M. Bodon leg. 15.1.1983, 32T NQ 0416, M. Bodon leg. 3.12.1983 (Figs. 146, 153, 154); shell of *Prespolitorea valvataeformis* Radoman, 1973a, from Lake Prespa, 3 Km north of Otesevo, Macedonia, *ex* W. J. M. Maassen collection (Fig. 156). Figs. 141, 143, 156: shell; Figs. 142, 144: outer face (Fig. 142 left, Fig. 144), profile (Fig. 142 centre) and inner face (Fig. 142 right) of operculum; Figs. 145–147: renal and pallial oviduct of three females; Fig. 148: intestine and pallial organs of a male; Fig. 149: renal and pallial oviduct, intestine and pallial organs of a female; Fig. 150: head of a male; Figs. 151–155: dorsal side of penis of six males. Scale bar = 1 mm.

Sees [Lake Ohrid]", Macedonia. According to Radoman (1983: 79), the type locality is "Lake Ohrid, on bank stones by Veli Dab. Spread along all the rocky east lake bank, exclusively on stones".

Type Material: Hadžišče (1959) did not give any information about the type material.

Material Examined

–H. Gorica, Lake Ohrid, Macedonia, 34T DL 84, 5. 1975, *ex* W. J. M. Maassen collection (2 shells with operculum, 2 shells).

Description

Shell very small, valvatiform, sometimes depressed; microsculpture of protoconch unknown; spire slightly raised, consisting of 2.75–3 rather rapidly growing, convex whorls; last whorl, large, dilated, more or less descending near aperture; umbilicus wide; aperture prosocline, ovoid to pyriform, moderately angled at its upper vertex, its external margin slightly concave at upper half; peristome complete, thin, slightly reflected only at columellar margin (Fig. 141; Hadžišče, 1959: 77–78, fig. 14; Radoman, 1963a: fig. 6a; 1963b: fig. 6a; 1983: 79, pl. 5, fig. 74). Dimensions: height = 0.65-0.80 mm; diameter = 1.08–1.20 mm (Radoman, 1983: table 5).

Operculum rather thick, yellowish red, paucispiral, thicker at centre of inner face, without peg (Fig. 142; Hadžišče, 1959: 78).

Body pigmentation not described; eye spots present (Hadžišče, 1959: fig. 14)

Male genitalia with penis rather elongated, conical, moderately pointed, and with one, rather evident, pointed lobe on left side about 2/3 of penis length (Hadžišče, 1959: 79, fig. 14; Radoman, 1963a: 78, fig. 14a; 1963b: 94, fig. 14a; 1983: 78, fig. 39).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle larger than distal, which is reduced; bursa copulatrix large, kidney-shaped, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1963a: 78, fig. 14a; 1963b: 94, fig. 14a; 1973a: 6; 1983: 40, 78, fig. 39).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and 4 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, their anterior margin with about 9 denticles; first marginal teeth rake-shaped, with row of about 20 denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying row of about 20 denticles (Hadžišče, 1959: 78–79, fig. 15; Radoman, 1963a: 90, fig. 17c; 1963b: 109, fig. 17c).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and slightly shorter pleuro-suboesophageal connectives (Radoman, 1973a: 6; 1983: 78).

Taxonomy

Ohrigocea is here considered a distinct genus, but its relationships to *Ohridohauffenia* Hadžišče, 1959, and possibly also *Karevia* Hadžišče, 1959, need to be clarified. *Ohrigocea* is characterized by: shell very small, valvatiform, depressed, sometimes carinate; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal larger than distal, which is rudimentary, and large, kidney-shaped bursa copulatrix with anterior duct; central tooth with one pair of basal cusps.

Ohridosturanya Radoman, 1973a, regarded by Radoman (1983) as a junior synonym of *Ohrigocea,* is not available. In fact, it was established by Radoman (1973b: 8; for *Horatia* (*Hauffenia*) *stankovici* Hadžišče, 1959) without a description or definition, but only by combining it with an available species-group name. After 1930, this condition does not make a generic name available (ICZN, 1999: Art. 13.6).

Radoman (1983: 78–80), assigned three other species to *Ohrigocea: O. karevi* Hadžišče, 1959, *O. miladinovorum* Hadžišče, 1959, and *O. stankovici* (Hadžišče, 1959). All are distinguished mainly by shell characters and live, together with *O. samuili,* in the Lake Ohrid.

Pezzolia Bodon & Giusti, 1986

Pezzolia Bodon & Giusti, 1986: 62–63.

Type Species: *Pezzolia radapalladis* Bodon & Giusti, 1986, by original designation.

Pezzolia radapalladis Bodon & Giusti, 1986

Pezzolia radapalladis Bodon & Giusti, 1986: 63–66, table 1, figs. 1A–G, pl. 1, figs. A–D, pl. 2, figs. A–D.

Type Locality: "spring inside the Rio di Tonnego, close to the Ponte della Vittoria, Rapallo, Genova. 3°14′34″N; 44°22′14″E; 30 m a.s.l. Square on the map of the Military Geographic Institute: 83 II SO, Rapallo", Italy.

Type Material: the holotype (SMF 305486, shell) is at the Senckenberg-Museum, Frankfurt am Main, Germany; paratypes (shells and preserved specimens) are at the Museo Civico di Storia Naturale G. Doria, Genoa, Italy, and in the Giusti (Siena, Italy), Bodon (Genoa, Italy), and Pezzoli (Milan, Italy) collections (Giusti & Pezzoli, 1981).

Material Examined

– Spring inside the Rio di Tonnego, Ponte della Vittoria, Rapallo, Genova, Liguria, Italy, 32T NQ 1613, M. Bodon leg. 16.12.1979, 31.12.1979, 29.11.1980, 3.12.1980, 4.4.1981, 3.4.1981, 16.5.1981, 4.10.1981, 6.11.1982 (8 males, 7 females, some specimens, many shells).
– Spring at Le Rocche, Casalino, Rapallo, Genova, Liguria, Italy, 32T NQ 1512, S. Gaiter leg. 28.8.1991 (1 female, many shells).
– Spring on right bank of the Bana Stream, below the tank of the Bana aqueduct, Camogli, Genova, Liguria, Italy, 32T NQ 1410, M. Bodon leg. 26.1.1992, 12.4.1992 (3 males, 5 females, some specimens, many shells).
– Cave Valdettaro no. 129 Li, Rapallo, Rapallo, Genova, Liguria, Italy, 32T NQ 1710, M. Bodon leg. 6.11.1992 (1 male, 3 females, 11 shells).
– Spring on left bank of the S. Francesco Stream, Il Campo, Rapallo, Genova, Liguria, Italy, 32T NQ 1913, M. Bodon leg. 31.3.1996, 15.12.1996 (2 males, 1 female, many shells).
– Spring on right bank of the Recco Stream, below the church of Avegno, Genova, Liguria, Italy, 32T NQ 1315, M. Bodon leg. 10.9.1994, 12.11.1994, 19.11.1996 (1 male, 3 females, a few shells).

For other localities where only shells have been collected see Pezzoli, 1988a.

Description

Shell very small, valvatiform, thin, whitish, waxen, transparent when fresh; surface of protoconch malleated; surface of teleoconch with thin growth-lines; spire raised, rarely depressed, planispiral, consisting of 2.5–3.25 rather rapidly growing convex whorls; last whorl large, slightly dilated, descending near aperture; umbilicus wide; aperture prosocline, oval or slightly pyriform; peristome complete, thin, slightly reflected only at columellar margin (Figs. 91, 143; Bodon & Giusti, 1986: 62–64, pl. 1, figs. A–D). Dimensions: height = 0.58–1.05 mm; diameter = 0.95–1.37 mm.

Operculum thin, pale yellowish, paucispiral, slightly thicker, but without traces of outgrowth at centre of inner face (Fig. 144; Bodon & Giusti, 1986: 62, 64, fig. 1C).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent (Fig. 150; Bodon & Giusti, 1986; 62, 64, fig. 1A, B).

Male genitalia with penis from short to elongated, flat, without lobes; penis terminal portion widening slightly before ending in short, pointed, conical-flat apex; penial duct zig-zagging through right portion of penis to open at penis tip (Figs. 151, 152; Bodon & Giusti, 1986: 62, 64, fig. 1B, G, table 1).

Female genitalia with two seminal receptacles and bursa copulatrix (when present) arising from distal renal oviduct; proximal seminal receptacle small, sometimes slightly smaller than distal; bursa copulatrix very reduced or absent, with very short duct so as to appear equal in size to distal seminal receptacle or sometimes smaller; seminal groove running along ventral side of capsule gland (Figs. 147, 149; Bodon & Giusti, 1986: 62, 64, fig. 1E, F, table 1).

Radula with central tooth trapezoidal with long lateral wings and basal tongue; anterior margin with 15–19 denticles, central of which longer, larger; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 13–18 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 11–16 small denticles anteriorly; second marginal teeth scraper-shaped, with long and slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Bodon & Giusti, 1986: 62, 64, pl. 2, figs. A–D).

Stomach without posterior caecum; intes-

tine with well-developed S-like bend on pallial wall (Figs. 148–149; Bodon & Giusti, 1986: 62, 64, fig. 1D, E).

Osphradium oval or reniform; ctenidium absent (Figs. 148–149; Bodon & Giusti, 1986: 62, 64, Fig. 1D, E).

Nervous system unknown.

Taxonomy

Pezzolia is characterized by: shell very small, valvatiform; operculum without peg; penis with or without glandular lobe/s; female genitalia with two seminal receptacles, proximal equal or smaller than distal, and bursa copulatrix very reduced or absent; central tooth with one pair of basal cusps.

In the only population of *Pezzolia radapalladis* studied by Bodon & Giusti (1986), the bursa copulatrix was always present, but in other populations subsequently discovered, it may be extremely reduced or even absent (Fig. 147). Other populations of *Pezzolia* recently found in the subterranean waters of Liguria are distinct from *P. radapalladis* by virtue of conchological (more globose shell) and anatomical (penis with 1–2 glandular lobes) characters (Figs. 145, 146, 153–155). This may support the existence of more than one species of *Pezzolia* (Pezzoli, 1988a; Bodon et al., 1995b).

***Prespolitorea* Radoman, 1983**

Prespolitorea Radoman, 1983: 68.

Type Species: *Prespolitorea valvataeformis* Radoman, 1983, by original designation.

Prespolitorea valvataeformis Radoman, 1973a

Prespolitoralia [sic] valvataeformis Radoman, 1973a: 20–21.

Type Locality: "stony, south-west coast of Lake Prespa, on the stones in the shallow coastal zone", Macedonia.

Type Material: lectotype (BEO 120, shell) at the Prirodnjacki Muzej u Beograd, together with a paralectotype (BEO 121, shell) (Jovanović, 1991).

Material Examined

– Lake Prespa, 3 km north of Otesevo, Macedonia, 33T DL 94, *ex* W. J. M. Maassen collection (1 shell).

Description

Shell very small, valvatiform; surface of protoconch malleated; spire rather depressed, consisting of 3–3.5 rather rapidly growing, convex whorls; last whorl large, dilated, slightly descending near aperture; umbilicus moderately wide, sometimes partly covered by reflected columellar margin of peristome; aperture prosocline, irregularly ovoid, its external margin sinuous, somewhat angled at periphery; peristome complete, thin, slightly thickened, reflected at columellar margin (Fig. 156; Radoman, 1973a: 20–21; 1983: 68, pl. 4, fig. 60; Jovanović, 1991: pl. 4, fig. 28). Dimensions: height = 0.84–1.01 mm; diameter = 1.18–1.30 mm (Radoman, 1983: table 4).

Operculum probably without outgrowth, though not specified.

Body pigmented; eye spots present.

Male genitalia with penis large, flat, apically extended in rather pointed conical tip, and with one small pointed lobe on left side about 2/3 of penis length (Radoman, 1973a: 21; 1983: 68, fig. 31).

Female genitalia with two seminal receptacles and a bursa copulatrix; proximal seminal receptacle much larger than distal, which is rudimentary; bursa copulatrix large, globose, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1973a: 6, 21; 1983: 40, 68, fig. 31).

Radula with central tooth with one pair of basal cusps; other details unknown (Radoman, 1983: 40).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and shorter pleuro-suboesophageal connectives (Radoman, 1973a: 6; 1983: 68).

Taxonomy

As Radoman (1973a: 7, 20–21) established *Prespolitorea* without a description or definition, but only by combining it with two new species (one of which he designated as type species), this nominal genus was not made available in 1973 (ICZN, 1999: Art. 13.6). On the contrary, the two new nominal species are available (ICZN, 1999: Art. 11.9.3). *Prespolitorea* is here considered a distinct genus. However, some of its anatomical details are

unknown, and its relationships to other Balkan genera (especially *Daphniola* Radoman, 1973, and *Horatia* Bourguignat, 1887) require further study. *Prespolitorea* is characterized by: shell very small, valvatiform; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal larger than distal (which is rudimentary), and large, globose bursa copulatrix with anterior duct.

Radoman (1973a: 21) included in *Prespolitorea* the type species, endemic to Lake Prespa, and another species from Lake Malo, south of Lake Prespa, Albania, *P. malaprespensis* Radoman, 1973a, distinguished from *P. valvataeformis* by shell shape.

Pseudohoratia Radoman, 1967

Pseudohoratia Radoman, 1967: 149–151.
Type Species: *Valvata ochridana* Polinski, 1929, by original designation.

Pseudohoratia ochridana (Polinski, 1929)

Valvata (*Atropidina*) *ochridana* Polinski, 1929: 136–137.
Type Locality: "[Lake Ohrid]", Macedonia. According to Radoman (1983: 115): "Lake Ohrid, in the Chara zone in the Ohrid gulf".
Type Material: Polinski (1929) did not give any information about the type material.

Material Examined

–Lake Ohrid, Macedonia, 34T DL, *ex* P. Radoman collection (2 males, 1 female).

Description

Shell very small, valvatiform, thin, yellowish, glassy, transparent when fresh; surface of protoconch malleated; spire raised, consisting of 3–3.25 rather rapidly, regularly growing, convex whorls; last whorl large, slightly dilated, more or less descending near aperture; umbilicus from small to wide; aperture prosocline, roundish to oval; peristome complete, slightly thickened, slightly reflected only at columellar margin (Figs. 92, 157; Polinski, 1929: 136–137; 1932: 617, pl. 7, fig. 4; Radoman, 1953: 64–66, figs. 1–3, 8, table 1; 1955: 60, table 4, pl. 5, figs. 9–11; 1967: 149, fig. 1; 1983: 114, pl. 8, fig. 131). Dimensions: height = 0.94–1.30 mm; diameter = 1.00–1.39 mm (Radoman, 1983: table 7).

Operculum slightly thickened, reddish yellow, paucispiral, with small, not or slightly apically dilated peg at centre of inner face (Figs. 40, 159; Radoman, 1953: 66, fig. 4; 1955: 57–58; 1967: 149, fig. 1; 1983: 114)

Body unpigmented; eye spots present (Fig. 158).

Male genitalia with prostate gland bulging well into pallial cavity; penis cylindrical, elongated, tapering near apex, ending in rather pointed tip, with small, non-glandular lobe on left side about 2/3 of penis length; penial duct zig-zagging through right or central (near tip) portion of penis to open at penis tip (Figs. 160, 161; Radoman, 1955: 43–44, fig. 99; 1967: fig. 2c; 1983: 114, fig. 61D).

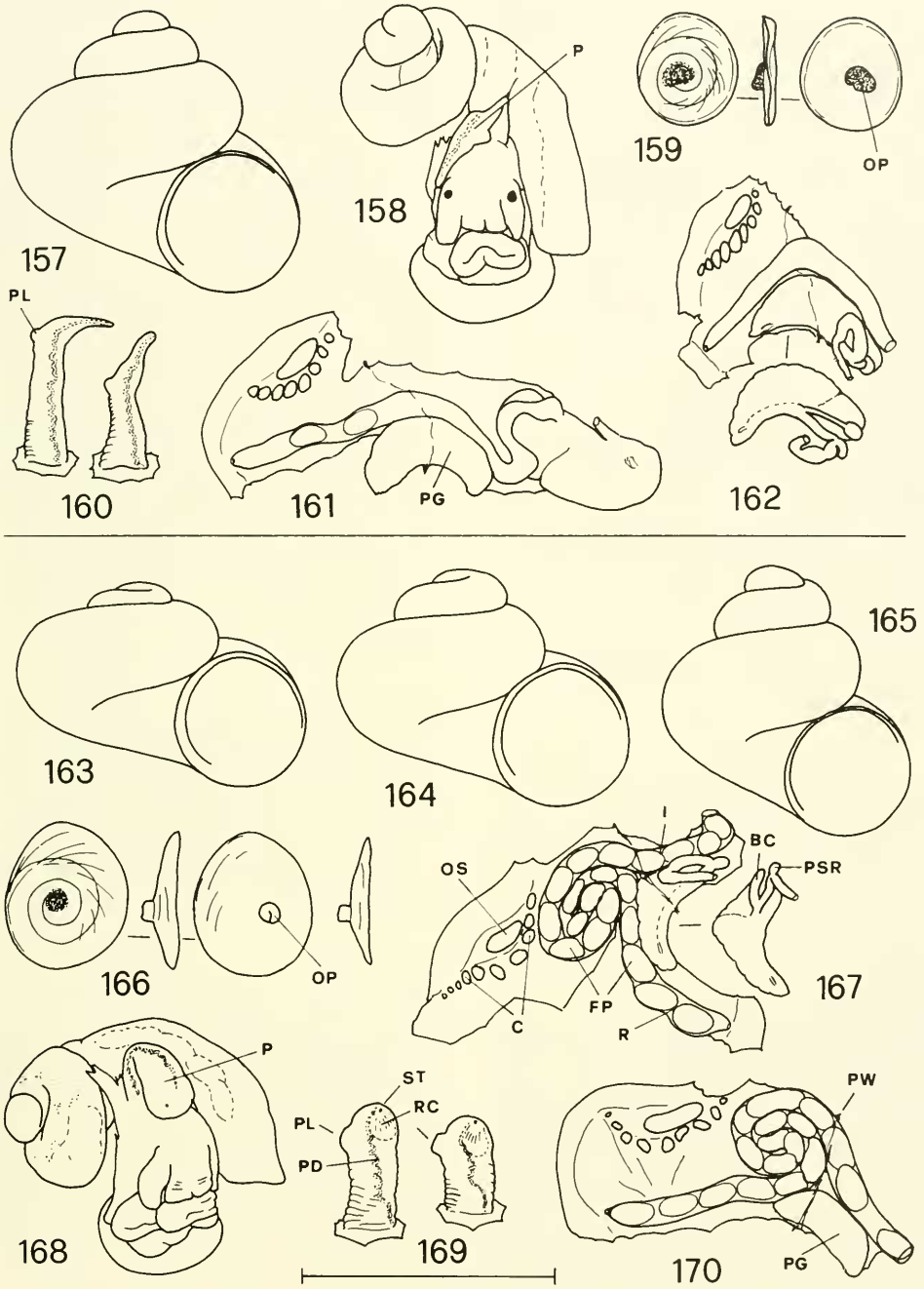
Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle small but proportionally rather developed, bent to adhere to oviduct; bursa copulatrix very small, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Fig. 162; Radoman, 1955: 36, 38–39, figs. 82, 83, 86–97; 1967: 150, fig. 2d; 1973a: 6, 10; 1983: 40, 114, fig. 61C).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and 3–4 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9–11 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 15–18 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Radoman, 1955: 12–13, fig. 17, table 2; 1967: 150, fig. 2a; 1983: 114, fig. 61A).

Stomach without posterior caecum; intestine without bend on pallial wall (Figs. 161, 162; Radoman, 1955: 21–24, figs. 34, 35; 1973a: 6; 1983: 40).

Osphradium variable in size, elongated, elliptical; ctenidium consisting of 7–9 lamellae (Figs. 161, 162; Radoman, 1955: 11, table 1).

Nervous system with long pleuro-supraoesophageal and shorter pleuro-suboesoph-



FIGS. 157–170. Shell, operculum and anatomical details of *Pseudohoratia ochridana* (Polinski, 1929) from Lake Ohrid, Macedonia, *ex* P. Radoman collection (Figs. 157–162) and of *Hauffenia wagneri* (Kuščer, 1928) from the spring of the "Vranja peč" cave, Boštanj, Sevnica, Krško, Slovenia, M. Bodon leg. 14.6.1985 (Figs. 163–170). Figs. 157, 163–165: shells; Figs. 158, 168: body of a male with pallial cavity open to show head and penis; Figs. 159, 166: outer face (left), profile (centre; also extreme right in Fig. 166) and inner face (right) of operculum; Figs. 160, 169: dorsal side of penis of two males; Figs. 161, 170: prostate gland, stomach (excluded in Fig. 170), intestine and pallial organs of a male; Figs. 162, 167: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

ageal connectives (Radoman, 1955: 45–46, fig. 123; 1967: 150, fig. 2b; 1973a: 6; 1983: 114, fig. 61B).

Taxonomy

Pseudohoratia is characterized by: shell very small, valvatiform; operculum with peg; penis with one simple lobe; female genitalia with proximal seminal receptacle and bursa copulatrix very small, but with long anterior duct; central tooth with one pair of basal cusps.

Horatia polinskii Radoman, 1953 (pp. 64–67, figs. 1–4; type locality: ". . . lac d'Ohrid . . . entre 20 et 120 m de profondeur . . .") is a junior synonym of *Pseudohoratia ochridana* (Polinski, 1929) according to Radoman (1983).

Radoman (1983: 115) included two more species from Lake Ohrid in *Pseudohoratia: P. brusinae* (Radoman, 1953) and *P. lacustris* (Radoman, 1964). They are distinguished by shell shape. Two out of 100 females of *P. brusinae* had a very rudimentary distal seminal receptacle (Radoman, 1983: 115).

Pseudoislamia Radoman, 1979

Pseudoislamia Radoman, 1979: 23.
Type Species: *Pseudoislamia balcanica* Radoman, 1979, by original designation.

Pseudoislamia balcanica Radoman, 1979

Pseudoislamia balcanica Radoman, 1979: 23–27, fig. 1, table 1, pl. 1, figs. 1, 2.
Type Locality: "Trichonis Lake, along the stone northeast bank, near by Mirtia, Greece".
Type Material: the lectotype (BEO 171, shell) is at the Prirodnjacki Muzej u Beograd together with a paralectotype (BEO 172, shell) (Jovanović, 1991).

Description

Shell very small, valvatiform, depressed; microsculpture of protoconch unknown; spire depressed, consisting of 2.75–3.25 rather rapidly growing convex whorls; last whorl large, dilated; umbilicus rather wide, deep; aperture prosocline, irregularly oval due to sinuous contour (upper part of external margin slightly concave; central part of external margin projected forwards, angled; lower margin convex); peristome complete, thin, slightly reflected only at columellar margin (Radoman, 1979: 23, 27, pl. 1, figs. 1, 2; 1983: 83, pl. 5, figs. 84–86; Jovanović, 1991: pl. 6, fig. 43). Dimensions: height = 0.84–1.05 mm; diameter = 1.18–1.34 mm (Radoman, 1979: table 1; 1983: table 5).

Operculum presumably without outgrowth though not specified.

Body pigmentation not described; eye spots present (Radoman, 1979: fig. 1; 1983: fig. 44).

Male genitalia with penis elongated, with one evident lobe on left side near apex (Radoman, 1979: 23, 27, fig. 1; 1983: 83, fig. 44).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal seminal receptacle slightly larger than distal; bursa copulatrix small, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1979: 6, 23, 27, fig. 1; 1983: 40, 83, fig. 44).

Radula with central tooth with one pair of basal cusps; other details unknown (Radoman, 1979: 23; 1983: 40).

Stomach without posterior caecum; intestine unknown (Radoman, 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and shorter pleuro-suboesophageal connectives (Radoman, 1979: 23; 1983: 83).

Taxonomy

The genus *Pseudoislamia* is characterized by: shell very small, valvatiform, depressed; operculum without peg; penis with one simple lobe; female genitalia with two seminal receptacles, proximal sligtly larger than distal, and very small bursa copulatrix with long anterior duct; central tooth with two pairs of basal cusps. It includes only the type species which is endemic to Lake Trichonis, Greece (Radoman, 1983).

Sardohoratia Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998

Sardohoratia Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998: 51–53.
Type Species: *Sardohoratia sulcata* Man-

ganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998, by original designation.

Sardohoratia sulcata Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998

Sardohoratia sulcata Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998: 53–55, figs. 28–30, 34–37, 40–45, 53–57.

Type Locality: "Plentiful karstic spring "Su Cologone" at San Giovanni, 100 m a.s.l. (Oliena, Nuoro). UTM references: 32T NK 4260", Sardinia, Italy.

Type Material: holotype (MZUF 11580, shell) and four paratypes (MZUF 11559, 11581, 4 shells) in the malacological collection of the Museo Zoologico "La Specola", Florence, Italy; other paratypes (145 shells and 14 preserved specimens) are in the Bodon (Genova, Italy), Cianfanelli (Florence, Italy), Giusti (Siena, Italy), Maassen (Duivedrecht, Holland), Sosso (Genoa, Italy), and Talenti (Florence, Italy) collections (Manganelli et al., 1998).

Material Examined

– Plentiful karstic spring "Su Cologone", San Giovanni, Oliena, Nuoro, Sardinia, Italy, 32T NK 4260, M. Bodon, F. Giusti & G. Manganelli leg. 22.11.1986 (44 shells), M. Bodon leg. 24.3.1989 (3 males, 4 females, 7 specimens, many shells).

Description

Shell very small, valvatiform, rather robust, whitish, waxen; surface of protoconch malleated surface of teleoconch with deep, scattered spiral groves; spire raised, consisting of 2.25–3 rather rapidly growing convex whorls; last whorl slightly dilated, not or slightly descending near aperture; umbilicus rather small; aperture prosocline, ovoid; peristome complete, thickened, columellar margin slightly reflected (Manganelli et al., 1998: 53–54, figs. 28–30, 34–37). Dimensions: height = 0.60–1.13 mm; diameter = 0.62–1.24 mm (Manganelli et al., 1998: table 1).

Operculum very thin, pale yellow, paucispiral, slightly thicker at centre, lacking outgrowth on inner face (Manganelli et al., 1998: 54, fig. 40).

Body unpigmented; eye spots absent (Manganelli et al., 1998: 54, fig. 41).

Male genitalia with penis rather elongated, slender, with pointed apex, without lobes; penial duct zig-zagging through central portion of penis to open at penis tip (Manganelli et al., 1998: 54, figs. 41–43).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; seminal receptacles of equal size; proximal seminal receptacle bent outwards near end of loop; bursa copulatrix large, oval, with rather long duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Manganelli et al., 1998: 54, figs. 44, 45).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and 5 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 20–22 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of approximately 12–15 small denticles (Manganelli et al., 1998: 54, figs. 53–57).

Stomach without posterior caecum; intestine with S-like bend on pallial wall (Manganelli et al., 1998: 54–55, figs. 42, 44).

Osphradium oval; ctenidium absent (Manganelli et al., 1998: 54–55, figs. 42, 44).

Nervous system unknown.

Taxonomy

The genus *Sardohoratia* is characterized by: shell very small, valvatiform; operculum without peg; penis without lobes; female genitalia with two seminal receptacles equal in size and large, oval bursa copulatrix with anterior duct; central tooth with one pair of basal cusps.

Besides the type species, *Sardohoratia* includes another species from Sardinia, *S. islamioides* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998, which differs in a few characters.

Strugia Radoman, 1973a

Strugia Radoman, 1973a: 10.

Type Species: *Strugia ohridana* Radoman, 1973a, by monotypy.

Strugia ohridana Radoman, 1973a

Strugia ohridana Radoman, 1973a: 10, 25.
Type Locality: "Cave from which Sum spring comes out, about 4 km west of town Struga, Macedonia".
Type Material: lectotype (BEO 262, shell) is at the Prirodnjacki Muzej u Beograd, together with a paralectotype (BEO 263, shell) (Jovanović, 1991).

Description

Shell very small, valvatiform; microsculpture of protoconch unknown; spire rather raised, consisting of 3.5–3.75 rather rapidly and regularly growing convex whorls; last whorl large, slightly dilated, more or less descending near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, slightly thickened, slightly reflected only at lower and columellar margin (Radoman, 1973a: 25; 1983: 118, pl. 8, fig. 139; Jovanović, 1991: pl. 8, fig. 65). Dimensions: height = 1.50–1.60 mm; diameter = 1.60–1.68 mm (Radoman, 1983: table 7).

Operculum reddish yellow, paucispiral, without outgrowth at centre of inner face (Radoman, 1973a: 25; 1983: 118).

Body unpigmented; eye spots absent (Radoman, 1983: 119).

Male genitalia with penis rather elongated, slightly dilated (at about 2/3 of penis length), then tapering to end in moderately pointed tip; small knob-like lobe on left side of penis level with subapical dilated portion (Radoman, 1983: 119, fig. 65).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle proportionally well developed, bent to adhere to oviduct; bursa copulatrix moderately large, sac-like or kidney-shaped, with rather long, slender duct entering bursa on anterior side; seminal groove running all along ventral side of capsule gland (Radoman, 1973a: 6, 25; 1983: 119, fig. 65).

Radula with central tooth with one pair of basal cusps; other details unknown (Radoman, 1983: 114).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40)

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and shorter pleuro-suboesophageal connectives (Radoman, 1973a: 6; 1983: 40, 118).

Taxonomy

Although Radoman (1973a: 10, 25) established *Strugia* without a description or definition, but only by combining it with a new species, this nominal genus is available (ICZN, 1999: Art. 13.4).

Strugia is here considered a distinct genus, but its relationships to *Lyhnidia* Hadžišče, 1959, need to be clarified. *Strugia* is characterized by: shell very small, valvatiform; operculum without peg; penis with one simple lobe; female genitalia with proximal seminal receptacle and large, sac-like or kidney-shaped bursa copulatrix with anterior duct; central tooth with two pairs of basal cusps.

A monotypic genus including only the type species, endemic to the Ohrid Basin.

Vrania Radoman, 1978

Vrania Radoman, 1978: 35, as subgenus of *Hauffenia*.
Type Species: *Valvata wagneri* Kuščer, 1928, by original designation.

Vrania wagneri (Kuščer, 1928)

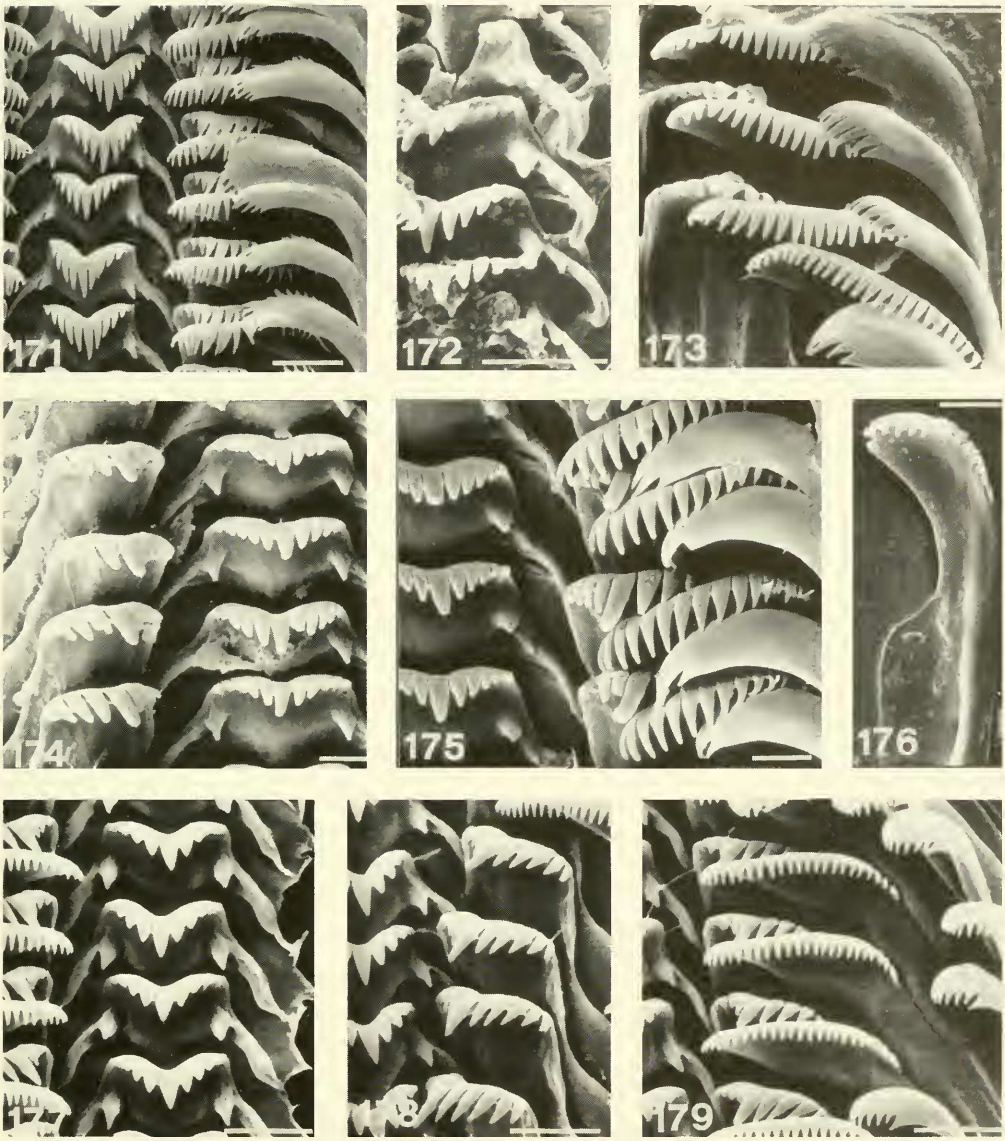
Valvata wagneri Kuščer, 1928: 50, fig. 1.
Type Locality: "Grotte Vranja peč bei Boštanj, 46°N, 15°7′E, Slovenia.
Type Material: Kuščer (1928) did not give any information about the type material.

Material Examined

– Spring of the "Vranja peč" cave, Boštanj, Sevnica, Krško, Slovenia, 33T WL 29, M. Bodon leg. 14.6.1985 (2 males, 2 females, 6 shells).
– Spodnja Klevevška Jama, S. 410, Smarjeta, Novo Mesto, Slovenia, 33T WL 18, F. Stoch leg. 16.6.1996 (1 female).

Description

Shell very small, markedly conical-valvatiform or valvatiform, thin, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire from moderately to well raised, consisting of 2.75–3.5 rather rapidly growing, convex whorls; last whorl dilated, sometimes descending slightly near aperture; umbilicus moderately wide; aper-



FIGS. 171–179. Radula of *Hauffenia wagneri* (Kuščer, 1928) from the spring of the "Vranja peč" cave, Bošanj, Sevnica, Krško, Slovenia, M. Bodon leg. 14.6.1985 (Fig. 171), *Fissuria raehlei* (Schütt, 1980) from well no. G/143, Poros, Cephalonia, Greece, G. L. Pesce, D. Maggi & G. Silverii leg. 2.4.1978 (Figs. 172, 173), *Islamia consolationis* (Bernasconi, 1985) from the cave Biez-Airoux, Consolation-Maisionnettes, Doubs, France, M. Bodon & G. Manganelli leg. 13.6.1996 (Figs. 174–176) and *Heraultia exilis* (Paladilhe, 1867) from the spring of Lez River, Hérault, France, M. Bodon leg. 2.12.1984 (Figs. 177–179). Figs. 171, 175: half of central portion of radula; Figs. 172, 177: central teeth; Figs. 173, 179: lateral, inner and outer marginal teeth; Fig. 174: central and lateral teeth; Fig. 176: outer marginal tooth; Fig. 178: four lateral teeth. Scale bar = 5 μm.

ture prosocline, roundish; peristome complete, thin, slightly reflected only at columellar margin (Figs. 93, 163–165; Kuščer, 1928: 50, fig. 1; Radoman, 1978: 35, pl. 4, figs. 16, 17; 1983: 122–123, pl. 9, fig. 145, table 7). Dimensions: height = 0.71–1.14 mm; diameter = 0.95–1.60 mm.

Operculum thin, yellowish, paucispiral, slightly thickened, with small, not apically dilated but spiralized peg at centre of inner face (Figs. 42, 43, 166; Bole, 1970: 92, fig. 2B5; Radoman, 1978: 35, fig. 5F; 1983: 122, fig. 67F).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent (Fig. 168).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather short, flat, with apex blunt, and one rather evident, wide lobe on left side near apex; penial duct zig-zagging through central portion of penis to open at penis tip; large, roundish or pyriform mass of refringent cells present inside penis apex right of penial duct; terminal part of penial duct (immediately before opening) with very small stylet (Figs. 169–170; Bole, 1970: 92, fig. 2B3).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle very small, sessile, or with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, small but longer than seminal receptacle, not or slightly dilated at apex, arising very close to where oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Fig. 167; Bole, 1970: 92, fig. 2B2).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5–6 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–12 denticles, central of which longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 21–24 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 14–19 very small denticles (Fig. 171; Bole, 1970: 92, fig. 2B4).

Stomach without posterior caecum; intestine with well-developed, tightly coiled, S-like bend on pallial wall (Figs. 167, 170; Radoman, 1978: 33; 1983: 40).

Osphradium variable in size, oval or elongated, kidney-shaped; ctenidium consisting of 7–11 lamellae (Figs. 167, 170; Bole, 1970: 92, fig. 2B1).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1978: 33; 1983: 120).

Taxonomy

Vrania is here considered a junior synonym of *Hauffenia* Pollonera, 1898 (see "The status and relationship of Hauffenia"). Radoman (1978) introduced this taxon, as subgenus of *Hauffenia*, for *Valvata wagneri* Kuščer, 1928. *Vrania* was confirmed as subgenus of *Hauffenia* by Radoman (1983) and Bole & Velkrovh (1986). On the contrary, Bole (1993) and Haase (1993) regarded it as a junior synonym of *Hauffenia.*

Vrania included only the type species.

Zaumia Radoman, 1983

Zaumia Radoman, 1983: 119.

Type Species: *Horatia kusceri* Hadžišče, 1959, by original designation.

Zaumia kusceri (Hadžišče, 1959)

Horatia kusceri Hadžišče, 1959: 65–66, figs. 4, 5.

Type Locality: "lebt in den Quellen des Klosters st. Naum am Südende des Sees und an den sechten, steinigen Teilen der Litoralregion auf der Ostseite des Sees", Ohrid Basin, Macedonia. According to Radoman (1983: 120), the type locality is "springs by Sveti Naum, near the south bank of Lake Ohrid".

Type Material: Hadžišče (1959) did not give any information about the type material.

Description

Shell very small, valvatiform or conical-ovoid, thin, glassy, transparent when fresh; microsculpture of protoconch unknown; spire well raised, consisting of 3.25–3.5 rather rapidly growing convex whorls; last whorl large, dilated, descending slightly near aper-

ture; umbilicus small, hole-like; aperture prosocline, roundish to ovoid; peristome complete, thin, slightly thickened, slightly reflected only at lower and columellar margin (Hadžišče, 1959: 65, fig. 4; Radoman, 1963a: 79, fig. 8; 1963b: 96, fig. 8; 1983: 119–120, table 7, pl. 8, fig. 140). Dimensions: height = 1.22–1.47 mm; diameter = 1.05–1.18 mm (Radoman, 1983: 206, table 7).

Operculum thin, paucispiral, without outgrowth at centre of inner side (Hadžišče, 1959: 65; Radoman, 1983: 119).

Body unpigmented; eye spots absent (Radoman, 1983: 120).

Male genitalia with penis long, cylindrical, slightly dilated at about 2/3 of penis length, then tapering to end in rather pointed tip; slightly evident lobe on left side, level with subapically dilated portion (Radoman's (1983: 119) diagnosis reports: ". . . without clear outgrowth") (Hadžišče, 1959: 65, fig. 4; Radoman, 1963a: fig. 16; 1963b: fig. 16; 1983: 119, fig. 66).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle small but proportionally rather developed; bursa copulatrix very small, with long, slender duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Radoman, 1963a: 79, fig. 16; 1963b: 96, fig. 16; 1973a: 6; 1983: 40, 114, 119, fig. 66).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long, robust central denticle and about 4 smaller denticles on both sides in decreasing order of size; one basal cusp at point where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with about 10 denticles, central of which longer and larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of about 20 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of very small denticles (Hadžišče, 1959: 65, fig. 5).

Stomach without posterior caecum; intestine unknown (Radoman, 1973a: 6; 1983: 40).

Osphradium and ctenidium unknown.

Nervous system with long pleuro-supraoesophageal and slightly shorter pleuro-suboesophageal connectives (Radoman, 1963a: fig. 18b; 1963b: fig. 18b; 1973a: 6; 1983: 119).

Taxonomy

Radoman (1973a: 8) established *Zaumia* without a description or definition, but only by combining it with two available species group names. After 1930, this condition does not make a generic name available (ICZN, 1999: Art. 13.6). *Zaumia* is here considered a distinct genus, but its relationships to *Pseudohoratia* Radoman, 1967, need to be clarified. *Zaumia* is characterized by: shell very small, valvatiform, conical-ovoid or depressed; operculum without peg; penis with one simple lobe; female genitalia with proximal seminal receptacle and very small bursa copulatrix, with long anterior duct; central tooth with one pair of basal cusps.

Radoman (1983) included another species from Lake Ohrid in *Zaumia: Z. sanctizaumi* (Radoman, 1964), distinct from *Z. kusceri* by valvatiform-planispiral shell.

STATUS AND RELATIONSHIPS OF *HAUFFENIA*

The western Palaearctic hydrobiids have rather constant anatomical organization, except for some features of the penis in males and the renal oviduct in females (Tables 1, 2, Fig. 180). Taxonomy at the rank of genus (and sometimes also at that of family) has thus been traditionally based on penis structure and the number and position of the sac-like structures associated with the renal oviduct (bursa copulatrix and seminal receptacle/s). The penis offers such characters as shape, presence of one of more lobes and their shape, glandular structures in the penis or lobes, papilla or filament at penis tip, stylet-like structures at penial duct opening, and position of penial duct inside penis. These characters are generally constant in groups of species and are therefore good diagnostic features at the rank of genus. However, cases are known in which some of these characters are absent in one species of a genus (e.g., *Pezzolia;* Fig. 180).

In supposedly related groups of species, the number and position of the sac-like structures associated with the renal oviduct, bursa copulatrix, and seminal receptacles (one or two) are considered more important (Davis & Carney, 1973). Also in this case, however, there are some exceptions, for example, the bursa copulatrix may be reduced, present or

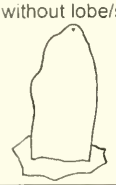
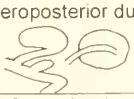
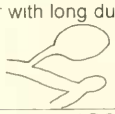
MALE / FEMALE		Penis with stylet	Penis without stylet		
		Penis with/ without lobe/s 	Penis with simple lobe/s 	Penis with glandular lobe/s 	Penis lacking lobe/s 
Seminal receptacle/s	Bursa copulatrix				
PSR + DSR 	Normal BC or with long duct 		*Bracenica* *Daphniola* *Gocea* *Horatia* *Karevia* *Ohridohauffenia* *Ohrigocea* *Prespolitorea* *Pseudoislamia*	*Fissuria*	*Sardohoratia*
	Reduced BC and duct 			*Pezzolia p.p.*	*Pezzolia p.p.*
	BC absent 		*Islamia p.p.*	*Islamia p.p.* *Pezzolia p.p.*	*Pezzolia p.p.*
Only DSR 	Normal BC with anterior duct 		*Kerkia*		*Arganiella*
	BC with posteroventral or lateroposterior duct 				*Hadziella* *Heraultia*
	BC smaller than DSR 				*Dabriana*
Only PSR 	Normal BC or with long duct 		*Lyhnidia* *Pseudohoratia* *Strugia* *Zaumia*		
	Reduced BC and duct 	*Hauffenia*			

FIG. 180. Synopsis of the European hydrobiid genera with valvatiform shell arranged according to the main anatomical characters of the genitalia (*Dalmatella* not included because anatomy unknown; it is identified by its keeled shell). The presence of the distal seminal receptacle needs to be confirmed in the type species of *Hadziella* (the genus is identified by its planispiral shell with reflected peristome). For each genus, only the characters of the type species or closely related species have been considered.
Acronyms: BC bursa copulatrix, DSR distal seminal receptacle (first seminal receptacle), PSR proximal seminal receptacle (second seminal receptacle).

TABLE 1. List of the main characters used in discussion of the status and relationships of *Hauffenia*. The character-state "0" was assigned to *Hydrobia*, because this genus is considered to be one of the primitive extant hydrobiids (Ponder, 1988a).

Protoconch	
P1	Surface depressions: absent (0); pits (1).
P2	Spirals: absent (0); spiral threads (1); spiral grooves (2).
P3	Wrinkles: absent (0); wrinkles or malleations (1).
Teleoconch	
T1	Shape: ovate-conic (0); planispiral (1); valvatiform (2); trochiform (3); neritiform (4); ovate (5); conic (6); elongate-conic (7).
T2	Spiralization: spire entirely coiled (0); despiralized only near aperture (1); almost entirely despiralized (2); horn-like, uncoiled (3).
T3	Whorl translation: apex of shell prominent (0); apex of shell flat (1).
T4	Whorl outline: flat (0); convex (1); shouldered (2).
T5	Color: absent (0); present (1).
T6	Microsculpture—Surface depressions: pits absent (0); pits present (1).
T7	Spiral microsculpture: absent (0); threads (1); grooves (2).
T8	Spiral sculpture: absent (0); crests (1); keel(s) (2).
T9	Axial sculpture: growth lines only (0); rounded ribs (1); lamelliform ribs (2).
T10	Spines: absent (0); present (1).
Aperture: peristome	
A1	Condition of outer lip relative to rest of apertural plan: simple (0); reflected (1); with varix at edge of outer lip (2); with varix behind outer lip (3).
A2	Shape of adapical and abapical portions of outer lip: simple (0); adapically sinuous (1); abapically sinuous (2); adapically and abapically sinuous (3).
A3	Inclination of outer lip relative to coil axis: orthocline (0); prosocline (1); opisthocline (2).
Umbilicus	
U1	Size: absent (0); narrow (1); wide (2).
Operculum	
O1	Overall shape: ovate (nucleus central or subcentral) (0); elongate-ellipsoid (nucleus submarginal) (1); circular (nucleus central) (2).
O2	Coiling: paucispiral (less than four whorls) (0); multispiral (four or more whorls) (1).
O3	Nuclear thickening and peg: nucleus simple (0); nucleus area thickened (1); nucleus raised into arched peg (2); nucleus raised into spiral peg (3).
O4	Crest on inner surface: inner surface simple (0); inner surface with crest (1).
O5	Frill: absent (0); slightly developed (1); highly developed (2); forming solid ridge (3).
Head-foot	
H1	Eyes: present, normal size (0); reduced (1); absent (2).
H2	Metapodial tentacle: absent (0); single tentacle present (1).
Pallial cavity	
C1	Posterior pallial tentacle: present (0); absent (1).
C2	Ctenidium: present (0); absent (1).
C3	Osphradium—size: more than 66% of pallial cavity length (0); 50–66% of pallial cavity length (1); less than 50% of pallial cavity length (2).
C4	Osphradium—position relative to ctenidium: opposite posterior part of ctenidium (0); opposite middle of ctenidium (1); opposite anterior part of ctenidium (2); inapplicable (ctenidium absent) (–).
C5	Osphradium—overall shape: more than three times longer than broad (0); two to three times longer than broad (1); less than twice as long as broad (2).
Radula	
R1	Central teeth—shape:trapezoidal (0); square (1); triangular (2); broadly rectangular (3).
R2	Central teeth—excavation of base: less than 25% of tooth height (0); 25%–50% of tooth height (1); more than 50% of tooth height (2).
R3	Central teeth—basal tongue length: absent (0); shorter than lateral wing (1); about equal to lateral wing (2); longer than lateral wing (3).
R4	Central teeth—basal tongue shape: narrow V-shaped (0); broad V-shaped (1); U-shaped to square (2); slightly convex (3).
R5	Central teeth—number of pairs of basal cusps: one pair (0); two pairs (1); three or more pairs (2); basal cusp absent (3).
R6	Central teeth—position of basal cusps: all cusps arise from lateral wing (0); one or more cusps arise from tooth face (1); inapplicable (basal cusps absent) (–).
R7	Central teeth—relative size of basal cusps: inner cusp larger (0); all cusps equal-size (1); inapplicable (one or no cusps) (–).

TABLE 1. (*Continued*)

R8	Lateral teeths—overall shape: outer margin straight or almost (0); outer margin with distinct concave bend (1).
R9	Lateral teeth—shape of face: taller than wide (0); square (1).
R10	Lateral teeth—basal projection: absent (0); present (1).
R11	Lateral teeth—length of cutting edge relative to outer wings: cutting edge much shorter (0); cutting edge slightly shorter to about equal in length (1).
R12	Inner marginal teeth—cusp size: cusp larger than those of outer marginal teeth (0); cusp about as large as those of outer marginal teeth (1).
Stomach	
S1	Posterior caecum: present (0); rudimentary or absent (1).
S2	Shield caecum: absent (0); present (1).
Intestine	
I1	Coiling: simple coil around style sac (0); coil around style sac with additional coil on dorsal side of style sac (1); simple coil far from style sac (2).
I2	Shape of rectum within pallial cavity: straight or with slight bend (0); with U-shaped bend (1); with S-shaped bend initiated to left (2); with S-shaped bend initiated to right (3).
Female reproductive system	
F1	Pigmentation of coiled oviduct: absent (0); present (1).
F2	Overall coiling pattern: single bend or loop (0); two or more bends or loops (1); no loop (2).
F3	Type A sperm duct: absent (0); present (1).
F4	Number and position of seminal receptacles: one distal (RS1) (0); one proximal (RS2) (1); two seminal receptacles (one proximal, one distal) (2); none (3).
F5	Relative size of seminal receptacles: distal (RS1) a little larger or equal to proximal (RS2) (0); distal (RS1) much larger than proximal (RS2) (1); distal (RS1) smaller than proximal (RS2) (2); inapplicable (one or no seminal receptacle) (–).
F6	Position of proximal seminal receptacle (RS2) relative to end of loop: at end of loop (0); close to end of loop (1); inapplicable (proximal seminal receptacle absent) (–).
F7	Position of proximal seminal receptacle (RS2) relative to bursa copulatrix: all or mostly anterior to bursa (0); lying against bursa (1); behind bursa (2); inapplicable (proximal receptacle or bursa absent) (–).
F8	Shape of proximal (RS2) seminal receptacle: elongate (0); pyriform to globular (1); inapplicable (proximal receptacle absent) (–).
F9	Duct of proximal (RS2) seminal receptacle: no distinct duct (0); distinct duct shorter than seminal receptacle (1); duct much longer than seminal receptacle (2); inapplicable (proximal receptacle absent) (–).
F10	Position of distal seminal receptacle (RS1) relative to end of loop: far from end of loop, near bursa copulatrix duct (0); closer to end of loop than to bursa copulatrix duct (1); inapplicable (distal seminal receptacle or bursa absent) (–).
F11	Position of distal seminal receptacle (RS1) relative to bursa copulatrix: all or most anterior to bursa (0); lying against bursa (1); behind bursa (2); inapplicable (distal receptacle or bursa absent) (–).
F12	Shape of distal (RS1) receptacle: elongate (0); pyriform to globular (1); inapplicable (distal receptacle absent) (–).
F13	Duct of distal (RS1) seminal receptacle: no distinct duct (0); distinct duct shorter than seminal receptacle (1); duct much longer than seminal receptacle (2); inapplicable (distal receptacle absent) (–).
F14	Dimension of posterior bursa copulatrix relative to albumen gland: medium to large (0); rather small (1); very small or rudimentary (2); inapplicable (no bursa) (–).
F15	Bursal duct: anteroventral (0); anterodorsal (1); anterior (2); posterodorsal (3); posteroventral or posterior (4); posterolateral (5); inapplicable (no bursa) (–).
F16	Opening: bursal duct opens into coiled oviduct (0); bursal duct opens into spermathecal duct (1); bursal duct opens into cordoseminal duct (2); inapplicable (no bursa) (–).
F17	Length of bursal duct: about 50–100% of bursa length (0); less than 50% of bursa length (1); longer than bursa (2); inapplicable (no bursa) (–).
F18	Glandular zones: homogeneous capsule gland (0); two or more glandular zones (1).
F19	Spermathecal duct: absent (0); common opening in capsule gland in anterior pallial cavity (1); opens separately to anterior pallial cavity (2); opens separately about halfway along capsule gland (3); opens separately to posterior pallial cavity (4).
F20	Ending of uteral gland: not far from pallial margin (0); far from pallial margin (1).
Male reproductive system	
M1	Overall shape of penis: gradually tapering (0); broadly triangular (1); rectangular (2); strap-like, i.e., flat (3).
M2	Shape of distal end: tapered (0); blunt (1); expanded (2); subapically expanded and tapered at tip (3).

TABLE 1. (*Continued*)

M3	Distal papilla: absent (0); present (1).
M4	Corneous stylet: absent (0); present, at tip (1); present, inside apex (2).
M5	Pigmentation of penis: absent (0); present (1).
M6	Simple lobe/s (non-glandular or glandular) on right or upper edge: absent (0); apical (1); lateral, in distal half (2); lateral, in proximal half (3).
M7	Simple lobe/s (non-glandular or glandular) on left edge: absent (0); apical (1); lateral, in distal half (2); lateral, in proximal half (3).
M8	Non glandular pleat on lower edge: absent (0), present (1).
M9	Glandular area inside simple lobe/s: absent (0), apocrine glands (1); internal glandular fields (2); inapplicable (no lobe) (–).
M10	External glandular fields or ridges: absent (0); present (1).
M11	Sucker-like apocrine glands: absent (0); present (1).
M12	Tubular penial gland—number: none (0); one (1); two or more (2).
M13	Tubular penial gland—position: absent (–); in penis only (1); in penis and haemocoel (2).
M14	Penial duct—position: near centre (0); near right edge (1).

absent in a genus (and also in a species, see the case of *Pezzolia*).

Clear relationships between *Hauffenia, Lobaunia, Neohoratia, Vrania* and *Erythropomatiana* emerge from the redescriptions of their type species. In fact, they share the following combination of characters:

- male genitalia with penis apex rounded; penial duct subcentral; terminal portion of penial duct (immediately before opening) with very small stylet; mass of refringent cells inside right side of penis apex; variable number (0-3) of more or less evident penial lobes on left side of penis near apex;
- female genitalia with bursa copulatrix and proximal seminal receptacle arising from distal renal oviduct; bursa copulatrix very small, with very short duct; proximal seminal receptacle shorter than bursa copulatrix.

This combination is unique and enables easy taxonomic identification of the *Hauffenia* group among all anatomically known valvatiform and non-valvatiform genera from all over the world (for the status and identification of all European valvatiform hydrobiid genera, see Tables 3, 4; Fig. 181).

Only two characters are available for the subdivision of *Hauffenia:* the opercular peg and the penial lobes. *Hauffenia* has an evident peg at the centre of the inner face of the operculum (very developed in *H. tovunica* Radoman, 1978, rather developed in *H. tellinii*), *Vrania* has a smaller peg, *Neohoratia* and *Erythropomatiana* lack a peg. As a first conclusion, *Erythropomatiana* can be proposed as a junior synonym of *Neohoratia.* Oddly, Radoman never considered or discussed *Neohoratia* when introducing (Radoman, 1978) and later redescribing (Radoman, 1983) *Erythropomatiana.* Radoman (1978, 1983) also included a species, *E. verdica* Radoman, 1978, which is a junior synonym of *N. subpiscinalis,* the type species of *Neohoratia* in *Erythropomatiana* (see Taxonomy in *Hauffenia subpiscinalis*).

Vrania was introduced as a subgenus of *Hauffenia* by Radoman (1978), on the basis of a single diagnostic character: the smaller opercular peg. Study of peg variations demonstrates that in specimens of *H. tellinii* from the type locality, the peg is more dilated apically and never as reduced as in *V. wagneri.* However, its dimensions vary over a continuum (Figs. 69–71) from that of *H. tellinii* to that of *V. wagneri.* Hence, the peg is not a character sufficient to support differentiation of *Vrania* with respect to *Hauffenia* at the rank of genus or subgenus. Together with other possible characters, it could at most support differentiation at species or subspecies level. In conclusion, we fully agree with Haase (1992) in considering *Vrania* a junior synonym of *Hauffenia.*

The remarkable concordance of the genital and other anatomical characters in *Hauffenia tellinii* and *Neohoratia subpiscinalis* and the variation of the opercular peg from very well developed in *H. tovunica* Radoman, 1978, to rather well developed in *H. tellinii,* and small in *V. wagneri,* throw doubts on the value of the character "peg absent" in *N. subpiscinalis* and *E. erythropomatia,* and consequently on the validity of *Neohoratia* (with *Erythropomatiana* as a junior synonym) as a generic taxon distinct from *Hauffenia* (with *Vrania* as a junior synonym).

Apart the absence of an opercular peg, *N.*

TABLE 2. Character states (see Table 1) in the European hydrobiid genera with valvatiform shell and in a selection of the best known European hydrobiid genera without valvatiform shell. The table also includes four taxa proposed as junior synonyms of *Hauffenia (Erythropomatiana, Neohoratia, Vrania,* and *Lobaunia*). For each genus, only the characters of the type species have been considered or those of the most closely related species, if the anatomy of the type species is not known. ? = no data.

	CHARACTERS																																				
TAXA	P1	P2	P3	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	A1	A2	A3	U1	O1	O2	O3	O4	O5	H1	H2	C1	C2	C3	C4	C5	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12
Arganiella	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	0	2	1	1	0	2	2	2	1	0	0	1	0	1	?	1
Bracenica	?	?	?	1	0	0	1	0	0	0	0	0	0	0	?	1	2	?	?	3	0	0	2	0	1	?	?	?	?	?	?	?	?	0	0	—	?	?	?	?	?
Dabriana	?	?	?	2	0	0	1	0	0	1	0	0	0	?	?	?	2	?	?	0	0	0	2	1	1	1	?	—	?	0	2	2	2	3	—	—	0	0	1	0	1
Dalmatella	?	?	?	2	0	0	2	0	0	0	2	0	0	0	?	1	2	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Daphniola	0	0	1	3	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	1	?	?	?	?	?	?	?	?	?	0	0	—	?	?	?	?
'Erythropomatiana"	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	12	0	1	0	2	1	1	0	2	1	1	01	0	—	1	?	?	?	1
Fissuria	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	0	2	1	1	0	?	?	?	1	0	0	0	0	?	?	1
Gocea	1	0	0	2	2	0	2	0	0	0	0	0	0	0	2	1	2	2	1	0	0	3	0	0	1	?	?	?	?	0	2	2	2	0	0	—	1	1	1	0	1
Hadziella	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	2	2	1	1	0	0	2	0	1	1	2	—	1	0	2	1	3	0	0	—	1	0	?	?	?
Hauffenia	0	0	1	12	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	3	0	0	2	0	1	01	2	1	1	0	2	2	1	01	0	—	1	0	1	0	1
Heraultia	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	2	2	0	0	0	0	2	0	1	0	2	1	1	0	2	1	3	0	0	—	1	0	?	?	1
Horatia	0	0	1	2	0	0	1	0	0	0	0	0	0	0	2	1	2	2	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	0	0	—	1	0	1	0	1
Islamia	?	?	?	3	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	0	0	—	1	?	?	?	1
Karevia	?	?	?	2	0	0	2	0	0	0	0	0	1	0	0	1	2	2	?	0	0	0	0	0	1	?	?	?	?	0	2	2	1	0	0	—	1	1	1	0	1
Kerkia	1	0	1	2	0	0	1	0	0	0	0	0	0	0	1	2	2	0	0	1	0	2	0	1	0	2	1	1	0	2	1	3	1	0	?	1	1	1	0	1
'Lobaunia"	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	0	?	?	?	0	2	1	1	01	0	0	?	?	?	?	1
Lyhnidia	?	?	?	3	0	0	1	0	0	0	0	0	0	0	2	1	1	2	0	0	0	0	0	0	1	?	?	?	?	0	2	2	1	0	0	—	1	1	1	0	1
'Neohoratia"	1	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	0	2	1	1	0	2	2	1	12	0	1	1	0	1	0	1
Ohridohauffenia	?	?	?	2	0	0	2	0	0	0	2	0	0	0	?	1	2	?	0	0	0	0	0	0	1	?	?	?	?	0	2	2	1	0	0	—	1	0	1	0	0
Ohrigocea	?	?	?	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	0	1	?	?	?	?	0	2	2	1	0	0	—	1	0	1	0	1
Pezzolia	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	1	2	—	1	0	2	2	2	0	0	—	1	0	1	?	1
Prespolitorea	?	?	?	2	0	0	1	0	0	0	0	0	0	0	0	1	2	?	?	0	0	0	0	0	1	?	?	?	?	?	?	?	?	0	0	—	?	?	?	?	?
Pseudohoratia	0	0	1	3	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	2	0	0	0	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	0	1
Pseudoislamia	?	?	?	2	0	0	1	0	0	0	0	0	0	0	?	1	2	?	?	0	0	0	0	0	1	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Sardohoratia	1	0	0	3	0	0	1	0	0	2	0	0	0	0	0	1	2	2	0	0	0	0	2	0	1	1	2	—	1	0	2	?	?	0	0	—	?	?	?	?	1
Strugia	?	?	?	2	0	0	1	0	0	0	0	0	0	?	?	?	2	?	0	0	0	0	2	0	1	?	?	?	?	?	?	?	?	0	0	—	?	?	?	?	?
'Vrania"	0	0	1	3	0	0	1	0	0	0	0	0	0	0	0	1	2	2	0	3	0	0	2	0	1	0	2	1	1	0	2	1	1	01	0	0	1	0	1	0	1
Zaumia	?	?	?	3	0	0	1	0	0	0	0	0	0	0	?	1	2	?	0	0	0	0	2	0	1	?	?	?	?	0	2	2	1	0	0	—	1	0	1	0	0
Adriohydrobia	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?
Alzoniella	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	1	0	2	1	1	0	2	2	?	0	0	—	0	?	?	?	1
Avenionia	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	2	1	1	0	2	2	1	0	0	—	1	0	1	0	1
Belgrandia	0	0	1	0	0	0	1	0	0	0	0	0	0	3	1	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	0	0	—	1	0	1	0	1
Belgrandiella	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	0	?
Bythinella	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	02	0	—	1	0	1	0	0
Bythiospeum	0	0	1	6	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	0	1
Clameia	0	1	0	7	1	0	1	0	0	1	0	0	0	1	1	0	1	?	?	?	?	?	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Graecoanatolica	0	0	0	6	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	?	?	?	?	0	1	2	2	2	1	?	?	?	?	?	?
Graziana	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	01	0	—	1	0	1	0	1

TABLE 2. (*Continued*)

TAXA	CHARACTERS																																									
	P1	P2	P3	T1	T2	T3	T4	T5	T6	T7	T8	T9	T10	A1	A2	A3	U1	O1	O2	O3	O4	O5	H1	H2	C1	C2	C3	C4	C5	R1	R2	R3	R4	R5	R6	R7	R8	R9	R10	R11	R12
Heleobia	0	0	1	6	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	?	?
Hydrobia	0	1	1	6	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	2	2	2	01	0	0	1	0	1	0	1
Iglica	0	1	1	7	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	1	2	—	1	?	?	?	?	?	?	?	?	?	?	?	?
Istriana	0	0	1	0	0	0	1	0	0	1	0	0	0	2	1	0	1	0	0	2	0	0	2	0	1	0	2	1	1	0	2	1	0	1	0	0	1	0	1	0	1
Lanzaiopsis	?	?	?	6	0	0	1	0	0	0	0	2	0	1	1	0	1	0	0	0	0	0	2	0	1	1	2	—	2	0	2	1	1	0	0	—	0	1	1	0	1
Lithoglyphus	0	0	0	4	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	2	?	?	0	2	1	2	2	1	0	1	0	1	1	1
Litthabitella	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	02	0	1	0	2	1	1	0	2	2	2	1	0	0	?	?	?	?	1
Marstoniopsis	0	2	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	1	0	0	2	2	2	1	0	0	1	0	1	0	1
Mercuria	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	0	2	2	1	01	0	—	1	0	1	0	0
Moitessieria	1	1	0	7	0	0	1	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	0	2	1	1	0	2	2	1	0	0	—	1	0	1	0	1
Orientalina	?	?	?	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	0	1
Palacanthiliopsis	?	?	?	6	0	0	1	0	0	1	0	0	0	1	1	2	1	0	0	2	0	0	2	0	1	0	2	1	1	?	?	?	?	0	0	—	?	?	?	?	?
Paladilhia	0	0	0	6	0	0	1	0	0	0	0	0	0	1	1	2	1	0	0	1	0	0	2	0	0	0	2	0	2	0	2	2	1	12	0	1	1	0	1	0	1
Paladilhiopsis	0	0	1	6	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	0	2	1	1	0	2	2	0	0	0	—	1	0	1	0	1
Pauluccinella	0	0	1	5	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	1	0	0	—	?	?	?	?	1
Phreatica	0	0	1	7	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	2	0	1	2	2	—	2	0	2	2	2	0	0	—	1	0	1	0	1
Plagigeyeria	?	?	?	6	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0	2	0	1	?	?	?	?	0	2	1	2	0	0	—	1	0	1	0	1
Potamopyrgus	0	1	1	6	0	0	0	1	0	0	0	0	01	0	0	0	01	0	0	0	0	0	0	0	1	0	2	1	0	0	1	2	3	2	1	0	1	0	1	0	?
Pseudamnicola	0	1	1	5	0	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	0	2	1	1	0	1	2	1	0	0	—	1	?	1	?	1
Pseudavenionia	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	12	0	1	01	2	1	1	0	2	2	1	01	0	—	1	?	?	?	1
Sadleriana	0	0	0	5	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	1	1	0	2	2	2	0	0	—	1	0	1	0	0
Sardopaladilhia	1	0	0	6	0	0	1	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	2	0	1	0	2	1	2	1	1	?	?	02	0	0	0	?	?	?	1

TAXA	S1	S2	I1	I2	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15	F16	F17	F18	F19	F20	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Arganiella	1	0	0	2	0	0	0	0	—	—	—	—	—	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	0	1	—	0	0	0	—	1
Bracenica	1	0	0	?	0	0	0	2	1	0	2	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Dabriana	1	0	0	?	0	0	0	0	—	—	—	—	—	1	2	1	1	2	2	0	1	1	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	1
Dalmatella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	?
Daphniola	1	0	0	?	0	0	0	2	2	0	1	1	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	0
"*Erythropomatiana*"	1	0	0	2	0	0	0	1	—	0	2	1	0	—	—	—	—	2	2	0	1	0	0	0	2	1	0	2	0	0	2	0	0	0	0	0	—	0
Fissuria	1	0	0	2	0	0	0	2	0	0	1	1	01	0	0	1	1	1	2	0	2	0	0	0	0	3	0	0	0	03	2	0	1	0	0	0	—	1
Gocea	1	0	0	?	0	0	0	2	0	0	1	0	0	0	0	1	1	0	1	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Hadziella	1	0	0	2	0	2	0	0	—	—	—	—	—	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	1
Hauffenia	1	0	0	2	0	0	0	1	—	0	2	1	0	—	—	—	—	2	2	0	1	0	0	0	2	1	0	2	0	0	02	0	—	0	0	0	—	0
Heraultia	1	0	0	1	0	0	0	0	—	—	—	—	—	0	0	0	1	0	5	0	2	0	0	0	1	0	0	0	0	0	0	0	—	0	0	0	—	1
Horatia	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	0
Islamia	1	0	0	1	0	0	0	2	2	1	—	1	1	—	—	1	1	—	—	—	—	0	0	0	2	0	0	0	0	0	1	1	2	0	0	0	—	1
Karevia	1	0	0	?	0	0	0	2	2	0	1	1	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Kerkia	1	0	0	2	0	0	0	0	—	—	—	—	—	0	0	0	0	0	1	0	0	0	0	0	2	3	0	0	0	0	2	0	0	0	0	0	—	1
"*Lobaunia*"	1	0	0	2	0	0	0	1	—	0	2	1	0	—	—	—	—	2	2	0	1	0	?	0	2	1	0	2	0	0	0	0	—	0	0	0	—	0

TABLE 2. (*Continued*)

TAXA	S1	S2	I1	I2	F1	F2	F3	F4	F5	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15	F16	F17	F18	F19	F20	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14
Lyhnidia	1	0	0	?	0	0	0	1	—	0	1	1	0	—	—	—	—	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
"*Neohoratia*"	1	0	0	2	0	0	0	1	—	0	2	1	0	—	—	—	—	2	2	0	1	0	0	0	2	1	0	2	0	0	2	1	0	0	0	0	—	0
Ohridohauffenia	1	0	0	?	0	0	0	2	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Ohrigocea	1	0	0	?	0	0	0	2	2	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Pezzolia	1	0	0	2	0	0	0	2	0	0	2	1	0	0	1	1	0	2	2	0	1	0	0	0	3	3	0	0	0	0	0	0	—	0	0	0	—	1
Prespolitorea	1	0	0	?	0	0	0	2	2	0	1	1	1	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	0
Pseudohoratia	1	0	0	0	0	0	0	1	—	0	1	1	0	—	—	—	—	2	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	0
Pseudoislamia	1	0	0	?	0	0	0	2	0	0	1	1	1	0	0	1	1	2	2	0	2	0	0	0	3	1	0	0	0	0	2	0	0	0	0	0	—	?
Sardohoratia	1	0	0	2	0	0	0	2	0	0	1	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	0
Strugia	1	0	0	?	0	0	0	1	—	0	1	1	1	—	—	—	—		2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Vrania"	1	0	0	2	0	0	0	1	—	0	2	1	0	—	—	—	—	2	2	0	1	0	0	0	2	1	0	2	0	0	2	0	0	0	0	0	—	0
Zaumia	1	0	0	?	0	0	0	1	—	0	1	0	0	—	—	—	—	2	2	0	2	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	—	?
Adriohydrobia	0	0	0	0	1	1	0	0	—	—	—	—	—	0	0	0	0	1	3	0	0	0	0	0	0	3	0	0	1	0	0	0	—	0	0	0	—	1
Alzoniella	1	0	0	2	0	0	0	2	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	3	0	0	0	3	0	1	1	0	0	0	—	1
Avenionia	1	0	0	0	0	0	0	2	1	1	1	0	1	0	0	1	0	0	0	0	1	0	0	0	2	0	0	0	0	3	1	0	1	0	0	0	—	1
Belgrandia	1	0	0	0	0	0	0	2	0	1	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	1	2	2	0	0	0	0	0	—	0
Belgrandiella	1	0	0	0	0	0	0	0	—	—	—	—	—	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	?	0	2	0	0	0	0	0	—	1
Bythinella	1	0	0	0	0	0	1	0	—	—	—	—	—	0	0	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	—	0	0	1	2	1
Bythiospeum	1	0	0	2	0	0	0	0	—	—	—	—	—	0	1	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	1
Clameia	1	0	2	0	0	0	0	0	—	—	—	—	—	0	1	1	2	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	—	0	0	0	—	?
Graecoanatolica	1	0	0	?	0	1	0	0	—	—	—	—	—	—	—	1	2	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	?
Graziana	1	1	0	0	0	0	0	0	—	—	—	—	—	0	1	0	0	0	2	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0	0	0	—	1
Heleobia	1	0	0	0	0	0	1	0	—	—	—	—	—	0	1	0	1	1	0	1	2	1	4	0	0	3	0	0	1	0	0	0	—	0	1	0	—	1
Hydrobia	0	0	0	0	1	1	0	0	—	—	—	—	—	0	0	0	1	1	1	0	2	0	0	0	2	2	0	0	1	0	0	0	—	0	0	0	—	1
Iglica	1	0	0	2	0	0	0	1	—	0	2	0	0	—	—	—	—	0	4	0	0	0	0	0	3	1	0	1	0	0	0	0	—	0	0	0	—	0
Istriana	1	0	0	0	0	0	0	0	—	—	—	—	—	0	1	1	1	0	2	0	0	0	0	0	3	1	0	1	0	0	0	0	—	0	0	0	—	1
Lanzaiopsis	1	0	?	?	0	0	0	0	—	—	—	—	—	0	1	0	1	0	4	0	0	0	0	0	1	0	0	0	0	0	0	0	—	0	0	0	—	0
Lithoglyphus	1	0	0	?	0	0	0	0	—	—	—	—	—	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	—	0	0	0	—	0
Litthabitella	1	0	0	0	0	0	0	2	0	0	1	1	0	0	1	1	1	0	04	0	0	0	0	0	3	0	0	0	0	0	1	0	2	2	0	0	—	1
Marstoniopsis	1	0	0	0	0	0	0	1	—	1	—	1	1	—	—	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	—	0	0	1	2	1
Mercuria	0	0	0	0	0	0	0	1	—	2	0	0	0	—	—	—	—	0	2	0	1	0	0	0	1	0	0	0	1	0	1	0	2	0	0	0	—	1
Moitessieria	1	0	2	0	0	0	0	3	—	—	—	—	—	—	—	—	—	0	4	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	—	0
Orientalina	1	0	0	0	0	0	0	2	0	0	1	0	1	0	0	0	0	0	2	0	0	0	0	0	0	3	0	0	0	0	2	0	0	0	0	0	—	0
Palacanthiliopsis	1	0	0	0	0	0	0	0	—	—	—	—	—	0	1	0	1	0	4	0	0	0	0	?	0	3	0	0	0	0	0	0	—	0	0	0	—	?
Paladilhia	1	0	2	0	0	0	0	1	—	1	1	1	1	—	—	—	—	0	4	0	0	0	0	1	0	0	0	0	0	0	0	0	—	0	0	0	—	?
Paladilhiopsis	1	0	0	0	0	0	0	0	—	—	—	—	—	0	1	0	0	0	4	0	0	0	0	0	0	3	0	0	0	0	0	0	—	0	0	0	—	1
Pauluccinella	1	0	0	0	0	0	0	2	0	1	—	0	1	—	—	0	0	—	—	—	—	0	0	0	0	0	0	0	1	2	2	0	0	0	0	0	—	1
Phreatica	1	0	0	0	0	0	0	0	—	—	—	—	—	0	2	1	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	0
Plagigeyeria	1	0	0	?	0	0	0	0	—	—	—	—	—	0	1	0	1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	0
Potamopyrgus	1	0	0	0	0	0	0	0	—	—	—	—	—	1	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	?
Pseudamnicola	0	0	0	0	1	0	0	0	—	—	—	—	—	0	0	0	0	0	1	0	2	0	0	0	1	1	0	0	1	0	0	0	—	0	0	0	—	1
Pseudavenionia	1	0	0	2	0	0	0	0	—	—	—	—	—	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	3	2	0	1	0	0	0	—	1
Sadleriana	1	0	0	0	0	0	0	2	0	1	1	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0	0	—	0
Sardopaladilhia	1	0	2	0	0	0	0	1	—	1	1	1	1	—	—	—	—	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	—	0	0	0	—	0

TABLE 3. Valvatiform hydrobiid taxa of the genus group from Europe and the Middle East (* taxa not discussed in the paper) and their taxonomic status according to the present revison or the recent literature.

Nominal taxon	Taxonomic status
Adriolitorea Radoman, 1973b, as *Islamia* (*Adriolitorea*)	junior synonym of *Islamia*
Arganiella Giusti & Pezzoli, 1980	*Arganiella*
Bracenica Radoman, 1973a	*Bracenica*
Dabriana Radoman, 1974	*Dabriana*
Dalmatella Velkovrh, 1970	*Dalmatella*
Daphniola Radoman, 1973a	*Daphniola*
*Daudebardiella** Boettger, 1905	*Daudebardiella**
Dolapia Radoman, 1983	junior synonym of *Karevia*
Erythropomatiana Radoman, 1978	junior synonym of *Hauffenia*
Fissuria Boeters, 1981	*Fissuria*
Gocea Hadžišče, 1956	*Gocea*
Hadziella Kuščer, 1932	*Hadziella*
Hauffenia Pollonera, 1898, as *Horatia* (*Hauffenia*)	*Hauffenia*
Heraultia n. gen.	*Heraultia*
Horatia Bourguignat, 1887	*Horatia*
Islamia Radoman, 1973a	*Islamia*
Karevia Radoman, 1973a (not Hadžišče, 1959)	junior synonym of *Ohrigocea*
Karevia Hadžišče, 1959, as *Ohrigocea* (*Karevia*)	*Karevia*
Kerkia Radoman, 1978	*Kerkia*
Lobaunia Haase, 1993	junior synonym of *Hauffenia*
Lyhnidia Hadžišče, 1959	*Lyhnidia*
Mienisiella Schütt, 1991	junior synonym of *Islamia*
Naumia Radoman, 1973a	name not available (see remarks to *Ohridohauffenia*)
Neohoratia Schütt, 1961a, as *Horatia* (*Neohoratia*)	junior synonym of *Hauffenia*
Ohridohauffenia Hadžišče, 1959, as *Ohridohoratia* (*Ohridohauffenia*)	*Ohridohauffenia*
Ohridosturanya Radoman, 1973a	name not available (see remarks to *Ohrigocea*)
Ohrigocea Hadžišče, 1959, as *Ohrigocea* (*Ohrigocea*)	*Ohrigocea*
Pezzolia Bodon & Giusti, 1986	*Pezzolia*
Prespolitorea Radoman, 1983	*Prespolitorea*
Pseudohoratia Radoman, 1967	*Pseudohoratia*
Pseudoislamia Radoman, 1979	*Pseudoislamia*
Rotondia Radoman, 1964, as *Pseudamnicola* (*Rotondia*)	name not available (see remarks to *Ohridohauffenia*)
Sardohoratia Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998	*Sardohoratia*
*Sheitanok** Schütt & Sesen, 1991	*Sheitanok*
Strugia Radoman, 1973a	*Strugia*
Vrania Radoman, 1978, as *Hauffenia* (*Vrania*)	junior synonym of *Hauffenia*
Zaumia Radoman, 1983	*Zaumia*

subpiscinalis and *E. erythropomatia* share another character state, the evident penial lobes, in the form of small pimples. *Vrania wagneri* apart from having a reduced opercular peg, is characterized by one evident wide penial lobe. *Hauffenia tellinii,* apart from having a rather developed opercular peg, is characterized by wide, but not evident penial lobes, or none at all. Three groups, based on two diagnostic characters, can therefore be identified.

The only anatomical difference between the four taxa consists in the different number and evidence of the penial lobes: 2–3, small, evident and roundish (*Neohoratia, Erythropomatiana*); 0–2, large but not evident (*Hauffenia*); one, evident and wide (*Vrania*). These differences are not sufficient for a distinction at the rank of genus or subgenus, in view of the marked variability in some of the type species studied by us (see above description and Figs. 22, 73–75, 84, 130, 138, 140, 169). We therefore propose *Neohoratia, Vrania, Erythropomatiana* as junior synonyms of *Hauffenia.*

Finally, with regard to *Lobaunia,* Haase's (1992) interpretation of its female genitalia

TABLE 4. Analytical key for the identification of the European valvatiform hydrobiid genera (*Dalmatella* is not included, because its anatomy is unknown; it is easily identified by its shell characters). For characters used, see Fig. 181.

1a — Three sac-like structures on renal oviduct: a bursa copulatrix (BC) and two seminal receptacles: distal (DSR) and proximal (PSR)	2
1b — Two sac-like structures on renal oviduct: a bursa copulatrix (BC) and a seminal receptacle (DSR or PSR) or two seminal receptacles (DSR and PSR)	12
2a — BC normal-sized, with evident duct	3
2b — BC reduced in size, not larger than a seminal receptacle, without evident duct; penis without lobe/s or with one or two glandular lobe/s	*Pezzolia* (in part) (Liguria, Italy)
3a — Penis with lobe/s	4
3b — Penis without lobe/s; PSR bent outwards	*Sardohoratia* (Sardinia Island, Italy)
4a — Penis with one simple lateral lobe	5
4b — Penis with 2–4 glandular lobes	*Fissuria* (France, Italy, and Greece)
5a — BC large, with duct about as long as BC	6
5b — BC small, with duct about twice as long as BC	*Pseudoislamia* (Greece)
6a — DSR slightly larger or smaller than PSR	7
6b — DSR much larger than PSR and about as long as bursa copulatrix duct; BC pyriform; operculum with peg	*Bracenica* (Montenegro)
7a — PSR distinct	8
7b — PSR relatively indistinct, bent to adhere to wall of oviduct	*Horatia* (Dalmatia and Macedonia)
8a — BC roundish	9
8b — BC not roundish	10
9a — PSR much larger than DSR	*Prespolitorea* (Prespa basin)
9b — PSR slightly larger than DSR	*Daphniola* (Greece)
10a — BC pyriform	11
10b — BC arched, kidney- or crescent-shaped; shell with two rows of raised nail-like projections	*Karevia* (Lake Ohrid)
11a — PSR larger than DSR	*Ohrigocea* and *Ohridohauffenia* (Ohrid basin)
11b — PSR about as long as DSR; last whorl of shell despiralized; operculum spiralized on outer face to resemble screw	*Gocea* (Lake Ohrid)
12a — Seminal receptacle (PSR) at end of loop of oviduct	13
12b — No seminal receptacle (PSR) at end of loop of oviduct (only DSR and BC beyond end of loop)	19
13a — BC normal-sized with evident duct, if reduced with long duct; penis with simple lobe	14
13b — BC reduced in size, without evident duct, or absent (in the latter case DSR present)	17
14a — Penial lobe large	15
14b — Penial lobe small	16
15a — BC medium-sized	*Lyhnidia* (Ohrid basin)
15b — BC very small	*Zaumia* (Ohrid basin)
16a — BC medium-sized	*Strugia* (Ohrid basin)
16b — BC very small; operculum with peg	*Pseudohoratia* (Lake Ohrid)
17a — BC slightly larger than PSR; wide penial apex with stylet and subcentral penial duct; operculum with or without peg	*Hauffenia* (Austria, NE Italy, and NW Balkans)
17b — BC absent and DSR not larger than PSR; penial apex without stylet and with lateral penial duct	18
18a — PSR usually larger than DSR and with evident duct; penis with one lateral or apical lobe, usually glandular	*Islamia* (France, Switzerland, S Europe, Turkey, Israel and Lebanon)
18b — PSR usually smaller than DSR and without evident duct; penis without or with one or two glandular lobe/s	*Pezzolia* (in part) (Liguria, Italy)
19a — BC larger than DSR	20
19b — BC small, smaller than DSR (which is very large); penis without lobe/s; caudal tentacle; central tooth of radula without basal cusps	*Dabriana* (Bosnia-Herzegovina)
20a — Duct of bursa copulatrix entering bursa on anterior side	21
20b — Duct of bursa copulatrix entering bursa on posteroventral or lateroposterior side; penis without lobe/s	22
21a — Penis with one simple lobe; operculum with crest on inner face	*Kerkia* (Slovenia)
21b — Penis without lobe/s; operculum at most with circular thickening at centre of inner face	*Arganiella* (Central Italy)
22a — Duct of bursa copulatrix entering bursa on posteroventral side; shell planispiral	*Hadziella* (NE Italy and NW Balkans)
22b — Duct of bursa copulatrix entering bursa on lateroposterior side	*Heraultia* (Hérault, France)

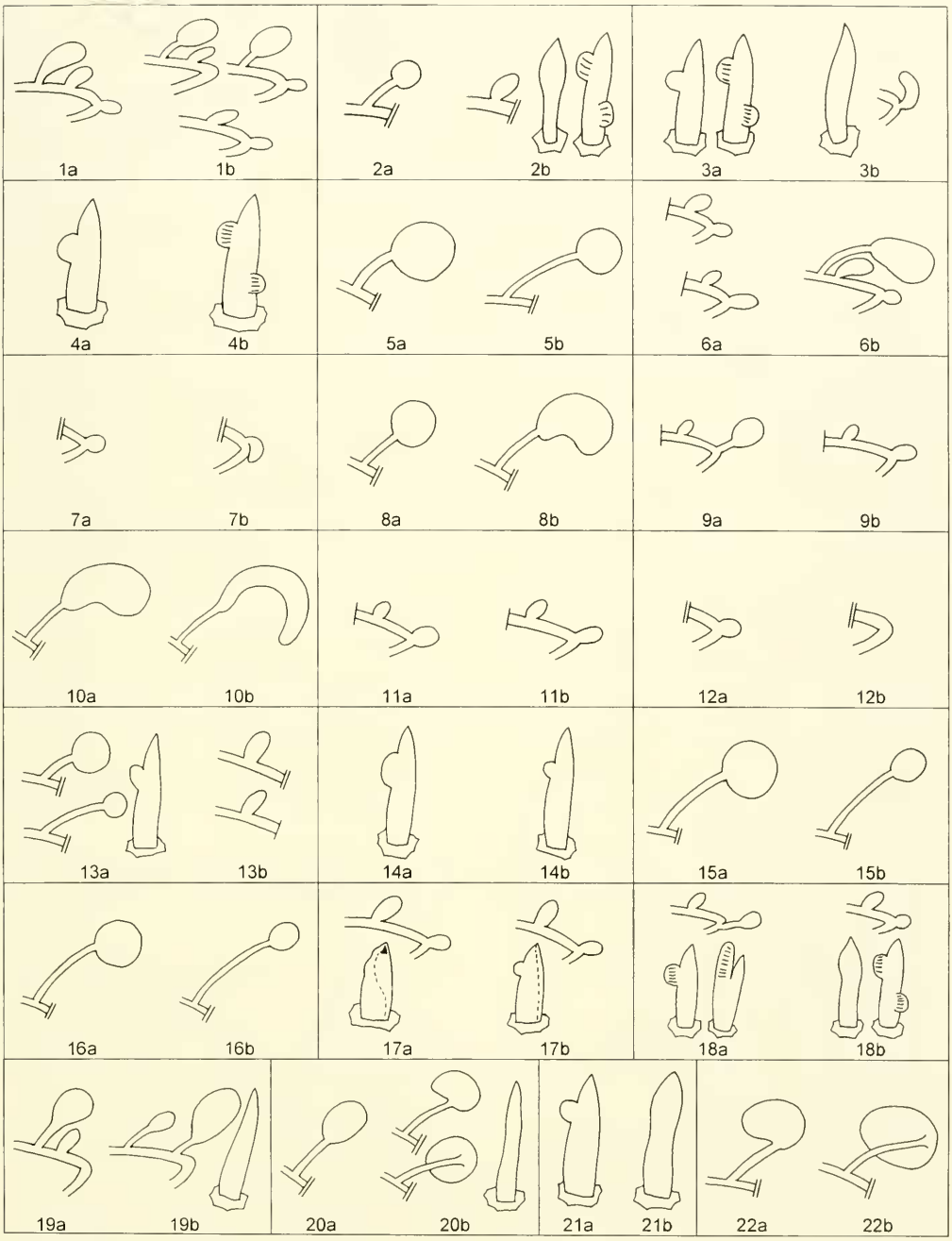


FIG. 181. Characters used in the analytical key for the identification of genera of European valvatiform hydrobiids (Table 4). The bar at the end of the oviduct means that another structure (bursa copulatrix or seminal receptacle) may be present; the double bar that two other structures (bursa copulatrix and seminal receptacle or two seminal receptacles) may be present.

needs confirmation. We propose this genus as a junior synonym of *Hauffenia*.

Concluding, the genus *Hauffenia* (including *Erythropomatiana, Neohoratia, Vrania* and *Lobaunia*) is characterized by: shell very small, conical-valvatiform to planispiral; operculum with or without peg; penis with stylet and with or without lobes; female genitalia with proximal seminal receptacle and very small bursa copulatrix; central tooth with one or two pairs of basal cusps.

We performed a parsimony analysis on a selection of European valvatiform and non-valvatiform hydrobiid genera in order to verify whether our conclusion about the affinities between *Hauffenia, Lobaunia, Neohoratia, Vrania* and *Erythropomatiana* was supported by synapomorphies. The data matrix consisted of a selection of 44 of the 62 taxa listed in Table 2. Sixteen genera were excluded because they were not well known (more than eight characters unknown: *Adriohydrobia, Bracenica, Clameia, Dabriana, Dalmatella, Daphniola, Graecoanatolica, Karevia, Iglica, Ohriohauffenia, Ohrigocea, Palacanthiliopsis, Prespolitorea, Pseudoislamia, Strugia* and *Zaumia*). All characters were assigned equal weight, and multistate characters were treated as nonadditive. Twenty-two of the 79 characters were parsimony uninformative: six were constant (T8, T10, H2, R10, M3, M13) and 16 were autoapomorphies (T2, T6, T9, O4, O5, C3, C4, R1, R11, S2, F2, F5, F10, F18, M10, M11). Character polarity was determined by outgroup comparison, choosing four different genera as outgroup: *Hydrobia* (subfamily Hydrobiinae), regarded as one of the most primitive extant genera (Ponder, 1988a); *Bythinella*, regarded as belonging to the family/subfamily Amnicolidae/Amnicolinae (Davis et al., 1985; Hershler & Thompson, 1988; Hershler & Ponder, 1988a); *Heleobia*, regarded as belonging to the subfamily Cochliopinae (= Littoridininae) (Davis et al., 1983; Hershler & Thompson, 1992; Hershler & Ponder, 1998); *Potamopyrgus*, regarded as possibly belonging to the distinct subfamily Potamopyrginae (Boeters, 1988; Ponder, 1988b).

1152 most parsimonious hypotheses were generated by our data matrix. All had 332 steps, with a Consistency Index of 0.425 and a Retention Index of 0.576 (Swofford, 1997). The strict consensus of the trees (Fig. 182) showed that 14 monophyletic groups appeared in all trees and that one of them was the *Hauffenia* group. If shell characters (P1-P3, T1-T10, A1-A3, U1) are excluded (most shell characters are considered to be plastic and subject to convergence; Ponder, 1988a), a total of 8208 most parsimonious hypotheses were generated by our data matrix. All had 250 steps, with a Consistency Index of 0.432 and a Retention Index of 0.571 (Swofford, 1997). The strict consensus of these trees (Fig. 183) showed that eight monophyletic groups appeared in all trees and that one of them was the *Hauffenia* group. In the two sets of trees, the *Hauffenia* group is always supported by the following synapomorphies: $F4_1$ [proximal seminal receptacle], $M2_1$ [penis with apex blunt], $M4_2$ [corneous stylet inside apex of penis] and $M14_0$ [penial duct running through central portion of penis], but only one of these, $M4_2$, is exclusive.

Shell characters played a major role in resolving phylogenetic relationships among the various genera (Fig. 182): when shell characters are omitted, resolution diminishes and some of the monophyletic groups disappear or change.

The cladistic analysis clearly produced a "non-result". Nevertheless, it was useful to show that morphological characters are not sufficient to reconstruct the phylogenesis of the hydrobiids. A combined approach, involving consideration of morphological and genetic data, is the only valid alternative.

STATUS OF THE SPECIES PRESENTLY ASSIGNED TO *HAUFFENIA*

Many species from different European localities (and even from outside Europe) have been assigned to *Hauffenia* and *Neohoratia* (Kuščer, 1932, 1933a, b; Bole, 1961, 1967a, b, 1979, 1993; Schütt, 1961b, 1962, 1980; Binder, 1966; Angelov, 1967; Radoman, 1973a, 1978, 1983; Bernasconi, 1975, 1977, 1984, 1985, 1988; Maassen, 1975, 1978; Boeters, 1973, 1974, 1981, 1988, 1998; Gittenberger, 1982; Bole & Velkovrh, 1986, 1987; Boeters & Rolan, 1988; Bech, 1990; Jovanović, 1991; Haase, 1992, 1993; Hinz et al., 1984; Rolan 1997a, b). Most of them, studied on the basis of shell characters only, followed in only a few cases by anatomical study, are in need of revision. As far as possible, we checked the status of each of them by studying any new material available.

Only a few species from the eastern Alps and Balkans actually belong to *Hauffenia* (for

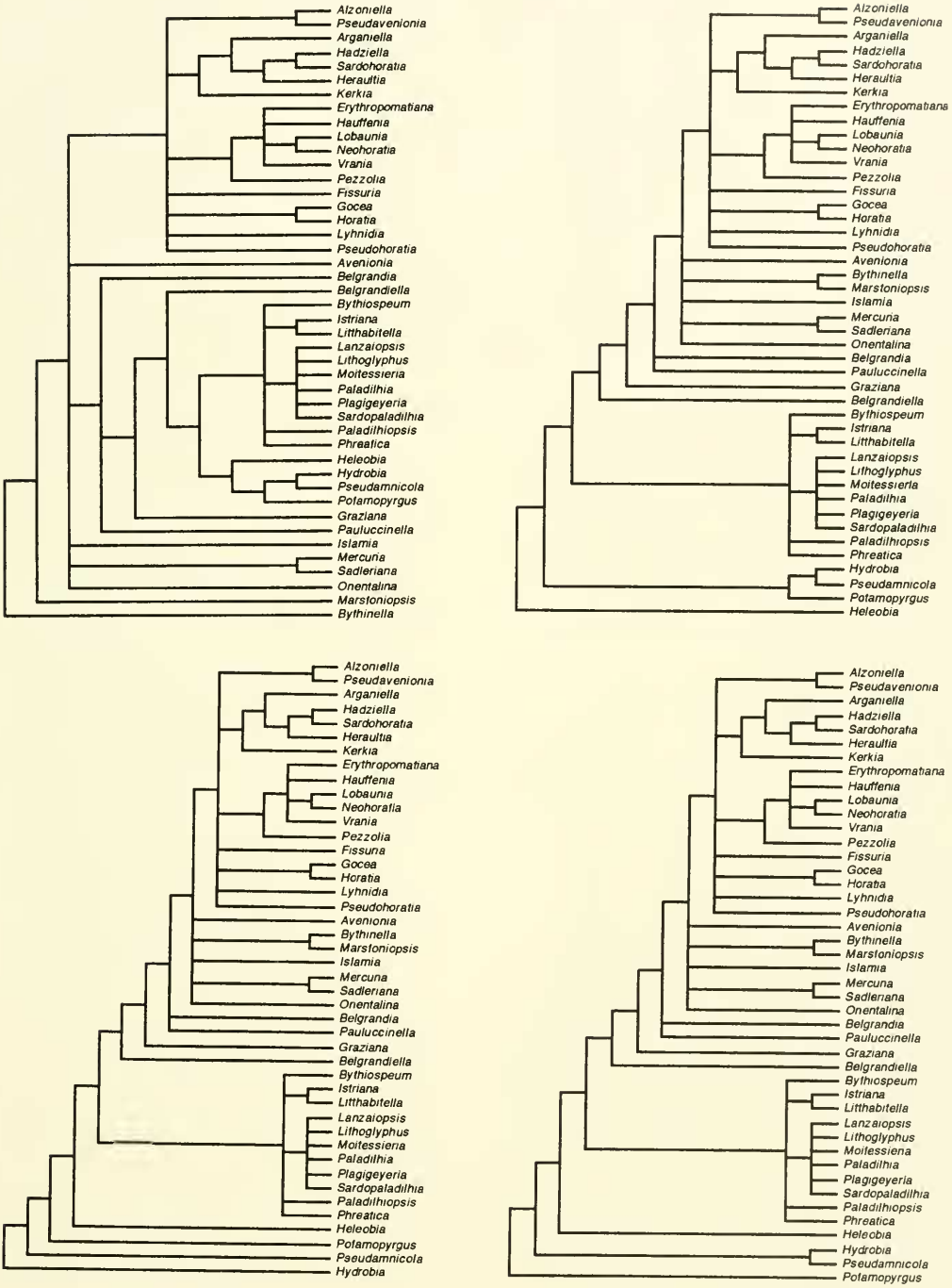


FIG. 182. The strict consensus trees of 1152 most parsimonious cladograms generated by the data matrix (Table 2) using *Bythinella, Heleobia, Hydrobia* and *Potamopyrgus* as outgroup for determining character polarity.

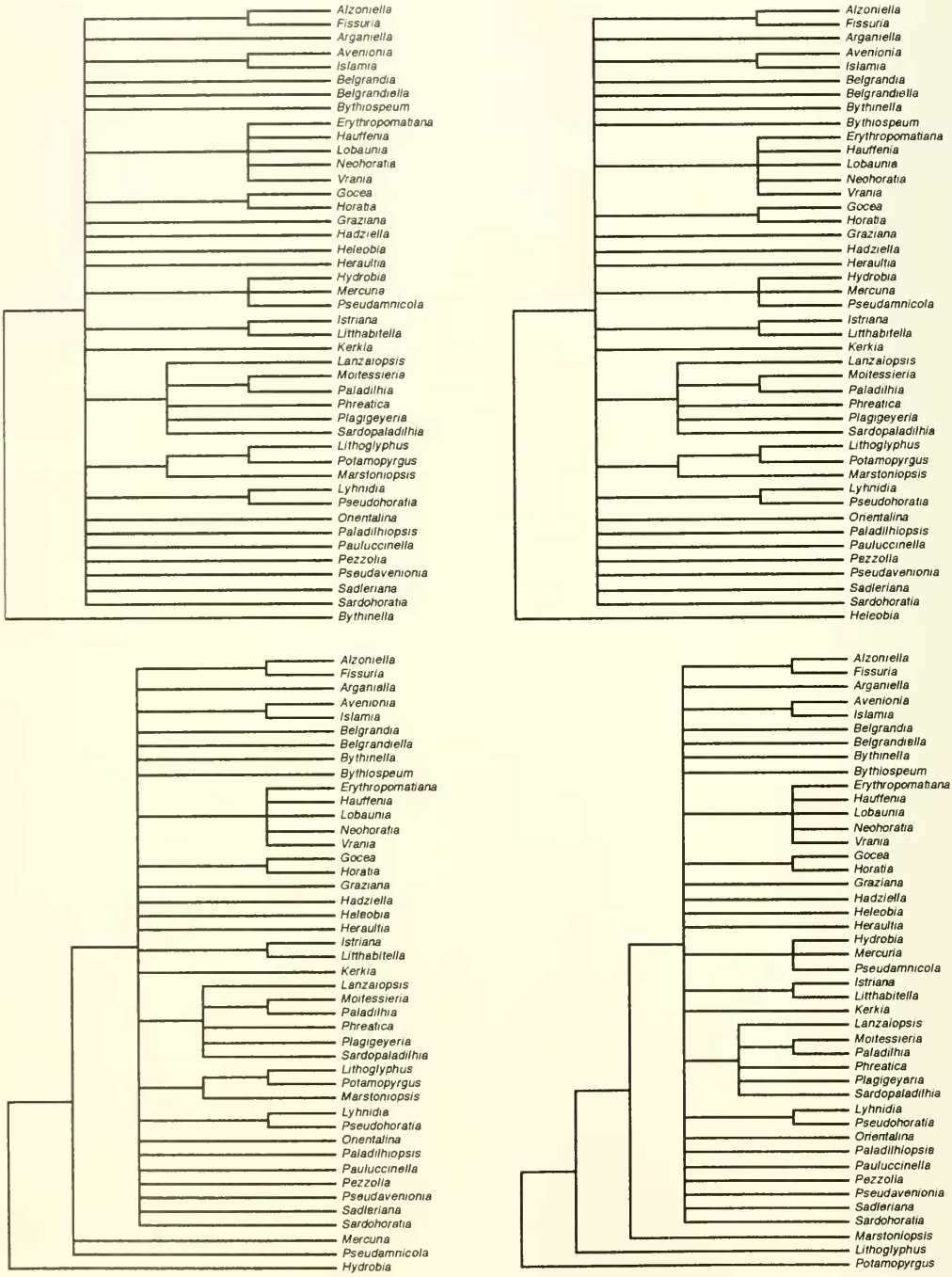


FIG. 183. The strict consensus trees of 8208 most parsimonious cladograms generated by the data matrix (Table 2) when shell characters (P1-P3, T1-T10, A1-A3 and U1) are excluded. Character polarity was determined by outgroup comparison, choosing four different genera as outgroup: *Bythinella, Heleobia, Hydrobia* and *Potamopyrgus*.

FIG. 184. Geographic range of the genus *Hauffenia* Pollonera, 1898 (only species certainly belonging to the genus are considered).

the distribution of *Hauffenia* and other European valvatiform hydrobiid genera, see Figs. 184–187; for the status and distribution of all European valvatiform hydrobiid species, see Tables 5, 6). In addition to the type species of *Hauffenia, H. tellinii* (Pollonera, 1898); *Erythropomatiana, H. erythropomatia* (Hauffen, 1856); *Neohoratia, H. subpiscinalis* (Kuščer, 1932); and *Vrania, H. wagneri* (Kuščer, 1928), they are: *H. kerschneri* (Zimmermann, 1930), *H. media* Bole, 1961, *H. subcarinata* Bole & Velkovrh, 1987, *H. tovunica* Radoman, 1978, and *H. wienerwaldensis* Haase, 1992. They are redescribed below (for their identification, see Table 7, Fig. 188).

The misidentified species will be discussed in four groups on the basis of their geographical distribution (central-eastern European species, French species, Spanish species, and North American species).

Central-Eastern European Species. Some nominal species described from the Balkan Peninsula are assigned to *Hauffenia* and to *Neohoratia* and listed as valid taxa by Bole & Velkovrh (1986), although all of them were overlooked by Radoman (1973, 1983). Their distribution far from Slovenia and northern Croatia (where species of *Hauffenia* live) throws serious doubt on their inclusion in *Hauffenia.*

They are: "*Hauffenia*" *edlaueri* (Schütt, 1961b), "*Hauffenia*" *jadertina* Kuščer, 1933a, "*Hauffenia*" *lucidula* (Angelov, 1967), "*Hauffenia*" *plana* Bole, 1961, "*Hauffenia*" *raehlei* (Schütt, 1980), "*Hauffenia*" *sinjana* (Kuščer, 1933a, "*Hauffenia*" *solitaria* Bole & Velkovrh, 1986 (*nomen nudum*), "*Neohoratia*" *epirana* (Schütt, 1962) and "*Neohoratia*" *hadei* (Gittenberger, 1982). For these species (except "*H.*" *lucidula,* "*H.*" *raehlei* and "*N.*" *epirana*),

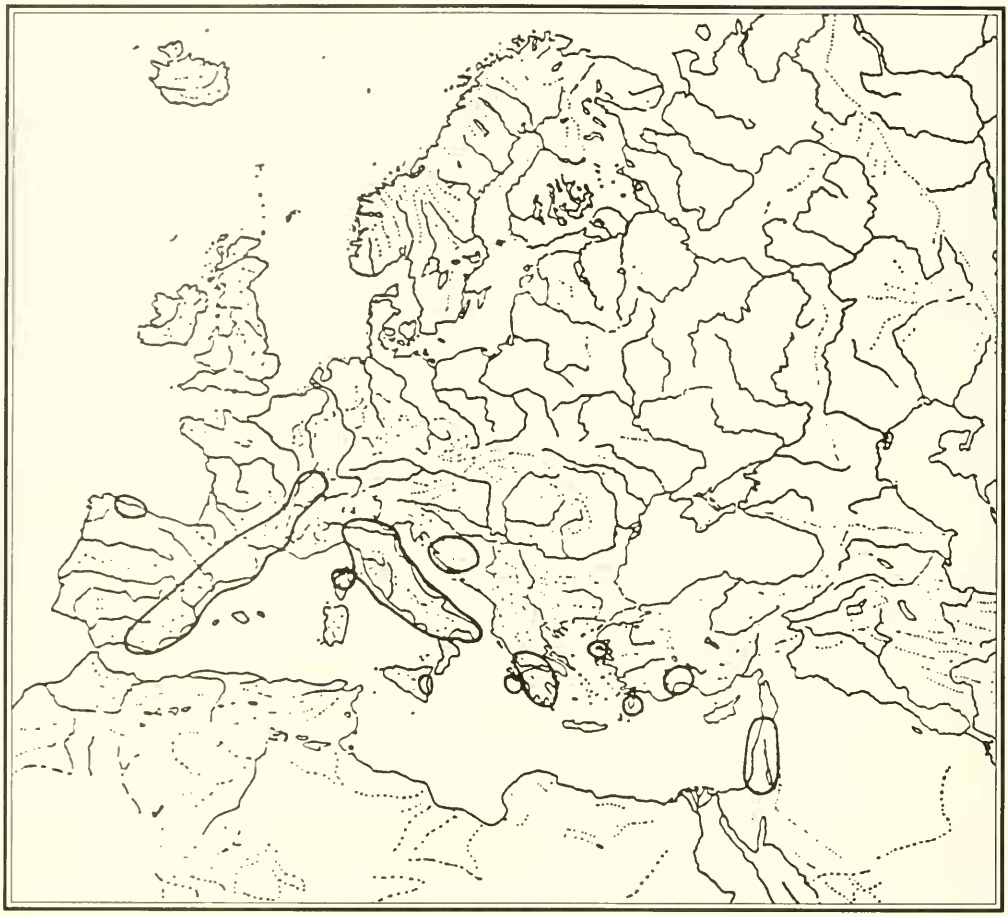


FIG. 185. Geographic range of the genus *Islamia* Radoman, 1973a. The distribution is probably wider in western and eastern Europe and Asia Minor, where little research has been carried out.

lack of anatomical data makes their inclusion in *Hauffenia* entirely speculative. In the case of "*H.*" *lucidula* and "*N.*" *epirana,* there is too little anatomical data available to make a positive generic arrangement. On the other hand, there is sufficient anatomical data on "*H.*" *raehlei* to allocate it to another genus, namely *Fissuria* (see *Fissuria raehlei* in the "Descriptions of some taxa misidentified as *Hauffenia* species").

French Species. Several very small, valvatiform, freshwater prosobranch gastropods from France were described under the generic name *Valvata* at the dawn of modern malacology: *V. minuta* Draparnaud, 1805; *V. moquiniana* Dupuy, 1851; *V. globulina* Paladilhe, 1866; *V. exilis* Paladilhe, 1867; *V. bourguignati* Letourneux, 1869; *V. micrometrica* Locard, 1889; and *V. turgidula* Locard, 1889.

Germain (1913, 1931) made the first revision, confirming only four species as valid: *V. minuta* (with *V. turgidula* as a junior synonym or form), *V. globulina* (with *V. bourguignati* and *V. micrometrica* as junior synonyms), *V. moquini* [*sic*] and *V. exilis.* More recently, Binder (1966) regarded *V. minuta* and *V. globulina* as belonging to the same, very variable species. On the basis of available conchological and

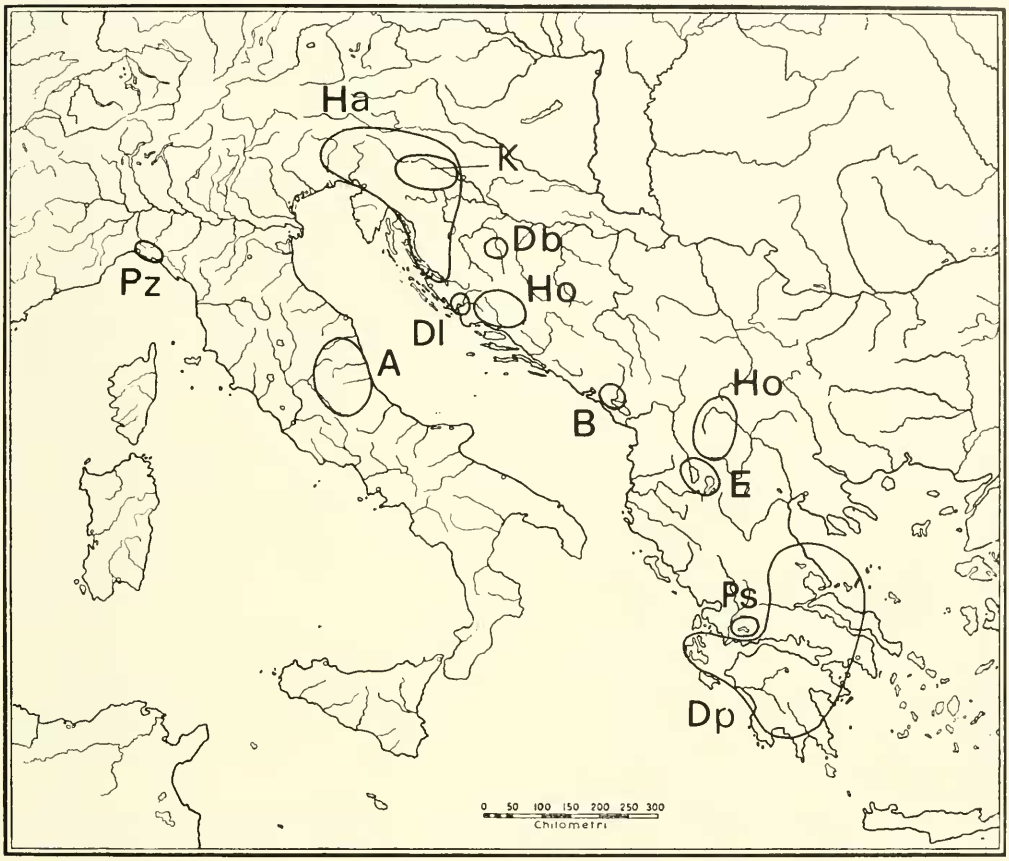


FIG. 186. Geographic range of the genera *Arganiella* Giusti & Pezzoli, 1980 (A), *Bracenica* Radoman, 1973a (B), *Dabriana* Radoman, 1974 (Db), *Dalmatella* Velkovrh, 1970 (Dl), *Daphniola* Radoman, 1973a (Dp), *Hadziella* Kuščer, 1932 (Ha), *Horatia* Bourguignat, 1887 (Ho), *Kerkia* Radoman, 1978 (K), *Pezzolia* Bodon & Giusti, 1986 (Pz), *Pseudoislamia* Radoman, 1979 (Ps) and endemic genera of Ohrid and Prespa basins (E) (*Gocea* Hadžišče, 1956, *Karevia* Hadžišče, 1959, *Lyhnidia* Hadžišče, 1959, *Ohridohauffenia* Hadžišče 1959, *Ohrigocea* Hadžišče, 1959, *Prespolitorea* Radoman, 1983, *Pseudohoratia* Radoman, 1967, *Strugia* Radoman, 1973a, *Zaumia* Radoman, 1983).

anatomical characters, he demonstrated that this species was a hydrobiid, which he assigned to *Hauffenia*.

Bernasconi (1975, 1977, 1984, 1985, 1988) revised the French *Hauffenia* and concluded that only one species, *Hauffenia* (*Neohoratia*) *minuta* (Draparnaud, 1805), lived in France. He regarded *V. globulina* and *V. moquiniana* as junior synonyms of *H. minuta*, and, following Boeters (1974), *V. exilis* as a species of *Horatia*. He split *H. minuta* into four subspecies, two of which he established: *H. minuta minuta, H. minuta globulina* (Paladilhe, 1866), *H. minuta spirata* Bernasconi, 1985, and *H. minuta consolationis* Bernasconi, 1985. The assignment of these taxa to *Hauffenia* (*Neohoratia*) was based on the small bursa copulatrix and single seminal receptacle (characters typical of *Hauffenia*) and on the absence of the opercular peg (a character considered typical of *Neohoratia*).

Unfortunately, Bernasconi's papers contain many mistakes, including misinterpretation of female genital structure. Our study of the French *Hauffenia* demonstrated that the two sac-like structures were two seminal receptacles, not a bursa copulatrix and a seminal receptacle. This and the structure of the penis (presence of glandular lobe on left side; absence of glandular mass in apical portion to right of penial duct; absence of stylet-like structure at tip) support inclusion of the

FIG. 187. Geographic range of the genera *Fissuria* Boeters, 1981 (F), *Heraultia,* n. gen. (H) and *Sardohoratia* Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998 (S).

French *Hauffenia* species in the genus *Islamia* (see "Descriptions of some taxa misidentified as *Hauffenia* species").

Our study supports placement of *V. exilis* in a new genus (see *Heraultia* n. gen. in "Description of a new valvatiform genus from France").

Spanish Species. In a recent revision of the western European hydrobiids, Boeters (1988) assigned a number of Iberian valvatiform species to two genera: *Horatia* and *Neohoratia.*

According to him, *Horatia* includes two Iberian species: *H. gatoa* Boeters, 1980; and *H.* (?) *sturmi* (Rosenhauer, 1856). The latter species was recently revised by Ramos et al. (1992) on topotypical material. None of these taxa belong to *Horatia,* notwithstanding the fact that they have a wide bursa copulatrix similar to that of species of *Horatia* (see description of *Horatia*). In fact, *Paludina sturmi* has the penis divided into a wide basal portion and a very long, slender tip with a small lobe near its base, and the female genitalia have only two sac-like structures: a large bursa copulatrix and a seminal receptacle (proximal or RS2) (Boeters, 1988: 220–221, figs. 160, 161, 172, 173; Ramos et al., 1992: 485). The same is true of *Horatia gatoa,* although this

TABLE 5. Valvatiform hydrobiid taxa of species group from Europe and the Middle East (* taxa not discussed in the paper) and their taxonomic status according to the present revision or the recent literature (when the generic name is in quotation marks, allocation of the taxon is dubious or very uncertain).

Nominal taxon	Taxonomic status
albanica, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
*amidicus**, *Sheitanok*—Schütt & Sesen, 1991	*Sheitanok amidicus**
*anatolica**, *Islamia*—Radoman, 1973a	*Islamia anatolica**
anti, Hadziella—Schütt, 1960	*Hadziella anti*
*asiana**, *Daudebardiella*—Boettger, 1905	*Daudebardiella asiana**
ateni, Microna—Boeters, 1969	*Islamia ateni*
azarum, Neohoratia—Boeters & Rolan, 1988	*Islamia azarum*
balcanica, Pseudoislamia—Radoman, 1979	*Pseudoislamia balcanica*
*bendidis**, *Islamia*—Reischütz, 1988	"*Islamia*" *bendidis**
*birsteini**, *Horatia*—Starobogatov, 1962	"*Horatia*" *birsteini**
*borutzkii**, *Horatia*—Zhadin, 1932	"*Horatia*" *borutzkii**
*bosniaca**, *Islamia*—Radoman, 1973a	*Islamia bosniaca**
bosniaca, Dabriana—Radoman, 1974	*Dabriana bosniaca*
boui, Fissuria—Boeters, 1981	*Fissuria boui*
bourguignati, Valvata—Letourneaux, 1869	possible junior synonym of *Islamia globulina*
brezicensis, Kerkia—Bodon & Cianfanelli, 1996	*Kerkia brezicensis*
brusinae, Horatia—Radoman, 1953	*Pseudohoratia brusinae*
*burnabasa**, *Horatia*—Schütt, 1964	*Islamia burnabasa**
cianensis, Islamia—Bodon, Manganelli, Sparacio & Giusti, 1995	*Islamia cianensis*
consolationis, Hauffenia minuta—Bernasconi, 1985	*Islamia consolationis*
coronadoi, Valvata—Bourguignat, 1870	"*Islamia*" *coronadoi*
danubialis, Lobaunia—Haase, 1993	*Hauffenia danubialis*
deminuta, Hadziella ephippiostoma—Bole, 1961	*Hadziella deminuta*
depressa, Pseudamnicola—Radoman, 1957	*Ohridohauffenia depressa*
drimica, Pseudamnicola (*Rotondia*)—Radoman, 1964	*Ohridohauffenia drimica*
edlaueri, Horatia (*Hauffenia*)—Schütt, 1961b	"*Hauffenia*" *edlaueri*
ephippiostoma, Hadziella—Kuščer, 1932	*Hadziella ephippiostoma*
epirana, Horatia (*Neohoratia*)—Schütt, 1962	"*Islamia*" *epirana*
erythropomatia, Valvata—Hauffen, 1856	*Hauffenia erythropomatia*
exigua, Valvata—Schmidt, 1856	*Daphniola exigua exigua*
exilis, Valvata—Paladilhe, 1867	*Heraultia exilis*
fezi, Valvata (?*Tropidina*)—Altimira, 1960	"*Islamia*" *fezi*
fontinalis, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
gaillardoti, Valvata (*Cincinna*)—Germain, 1911	*Islamia gaillardoti*
gaiteri, Islamia—Bodon, Manganelli, Sparacio & Giusti, 1995	*Islamia gaiteri*
gasulli, Hauffenia (*Neohoratia*)—Boeters, 1981	"*Horatia*" *gasulli*
gatoa, Horatia—Boeters, 1980	"*Horatia*" *gatoa*
gjorgjevici, Lyhnidia—Hadžišče, 1959	*Lyhnidia gjorgjevici*
gjorgjevici, Ohridohoratia (*Ohridohauffenia*)—Hadžišče, 1959	junior synonym of *Ohridohauffenia depressa*
globulina, Valvata—Paladilhe, 1866	*Islamia globulina*
globulus, Amnicola—Bofill, 1909	*Islamia globulus globulus*
*graeca**, *Islamia*—Radoman, 1973a	*Islamia graeca** (junior synonym of "*Islamia*" *epirana?*)
graeca, Daphniola—Radoman, 1973a	junior synonym of *Daphniola exigua exigua*
hadei, Horatia (*Neohoratia*)—Gittenberger, 1982	"*Hauffenia*" *hadei*
hadzii, Lyhnidia—Hadžišče, 1959	*Lyhnidia hadzii*
hellenica, Valvata (*Cincinna*)—Westerlund, 1898	junior synonym of *Daphniola exigua exigua*
islamioides, Sardohoratia—Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998	*Sardohoratia islamioides*
jadertina, Hauffenia—Kuščer, 1933a	"*Hauffenia*" *jadertina*
karamani Lyhnidia—Hadžišče, 1959	*Lyhnidia karamani*
karevi, Ohrigocea (*Ohrigocea*)—Hadžišče, 1959	*Ohrigocea karevi*
kerschneri, Horatia erythropomatia—Zimmermann, 1930	*Hauffenia kerschneri*
klecakiana, Horatia—Bourguignat, 1887	*Horatia klecakiana*
*knorri**, *Horatia*—Schütt, 1961	"*Horatia*" *knorri*

TABLE 5. (*Continued*)

Nominal taxon	Taxonomic status
krkae, Hadziella—Bole, 1992	*Hadziella krkae*
kusceri, Hauffenia—Bole, 1961	*Kerkia kusceri*
kusceri, Horatia—Hadžišče, 1959	*Zaumia kusceri*
lacustris, Pseudamnicola (*Rotondia*)—Radoman, 1964	*Pseudohoratia lacustris*
lagari, Pseudamnicola—Altimira, 1960	*Islamia globulus lagari*
*latina**, *Islamia*—Radoman, 1973a	*Islamia latina**
letourneuxi, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
*ljovuschkini**, *Horatia*—Starobogatov, 1962	"*Horatia*" *ljovuschkini**
loichiana, Hauffenia kerschneri—Haase, 1993	junior synonym of *Hauffenia kerschneri*
lucidula, Horatia (*Hauffenia*)—Angelov, 1967	"*Hauffenia*" *lucidula*
lucidulus [*sic*], *Horatia* (*Hauffenia*)—Angelov, 1967	"*Hauffenia*" *lucidula*
lyhnidica, Pseudamnicola (*Ohrigocea*)—Radoman, 1963a	junior synonym of *Ohrigocea stankovici*
macedonica, Sadleriana—Kuščer, 1936	*Horatia macedonica*
malaprespensis, Prespolitorea—Radoman, 1973a	*Prespolitorea malaprespensis*
media, Hauffenia—Bole, 1961	*Hauffenia media*
michleri, Hauffenia—Kuščer, 1932	junior synonym of *Hauffenia tellinii*
micrometrica, Valvata—Locard, 1889	possible junior synonym of *Islamia globulina*
mienisi, Mienisiella—Schütt, 1991	*Islamia mienisi*
miladinovorum, Ohrigocea (*Karevia*)—Hadžišče, 1959	*Ohrigocea miladinovorum*
*miljackae**, *Dalmatella*—Bole & Velkovrh, 1986	*nomen nudum*
minuta, Pseudamnicola—Radoman, 1955	*Ohridohauffenia minuta*
minuta, Valvata—Draparnaud, 1805	*Islamia minuta*
moquiniana, Valvata—Dupuy, 1851	possible senior synonym of *Islamia globulina*
*naegelei**, *Daudebardiella*—Boettger, 1905	*Daudebardiella naegelei**
novoselensis, Horatia—Radoman, 1966	*Horatia novoselensis*
obliqua, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
obtusa, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
ochridana, Valvata (*Atropidina*)—Polinski, 1929	*Pseudohoratia ochridana*
ohridana, Gocea—Hadžišče, 1956	*Gocea ohridana*
ohridana, Strugia—Radoman, 1973a	*Strugia ohridana*
ornata, Pseudamnicola—Radoman, 1957	*Karevia ornata*
palustris, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
pangaea, Horatia (*Daphniola*) *exigua*—Reischütz, 1984	"*Daphniola*" *exigua pangaea*
*parvulus**, *Lithoglyphus*—Naegele, 1894	"*Horatia*" *parvula**
pescei, Arganiella—Giusti & Pezzoli, 1980	*Arganiella pescei*
plana, Hauffenia—Bole, 1961	"*Hauffenia*" *plana*
planospira, "Fissuria"—Bodon, Cianfanelli & Talenti, 1997	"*Fissuria*" *planospira*
polinskii, Horatia—Radoman, 1953	junior synonym of *Pseudohoratia ochridana*
praeclara, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
prlitchevi, Ohrigocea (*Karevia*)—Hadžišče, 1959	junior synonym of *Karevia omata*
*pseudorientalica**, *Islamia*—Radoman, 1973a	*Islamia pseudorientalica**
pusilla, Valvata—Piersanti, 1952	*Islamia pusilla*
radapalladis, Pezzolia—Bodon & Giusti, 1986	*Pezzolia radapalladis*
raehlei, Horatia (*Hauffenia*)—Schütt, 1980	*Fissuria raehlei*
rotonda, Pseudamnicola (*Rotondia*)—Radoman, 1964	*Ohridohauffenia rotonda*
rudnicae, Hadziella—Bole, 1992	*Hadziella rudnicae*
samuili, Ohrigocea (*Ohrigocea*)—Hadžišče, 1959	*Ohrigocea samuili*
sandanskii, Ohrigocea (*Karevia*)—Hadžišče, 1959	junior synonym of *Karevia omata*
schuelei, Hauffenia (*Neohoratia*) *coronadoi*—Boeters, 1981	*Islamia schuelei*
servaini, Horatia—Bourguignat, 1887	junior synonym of *Islamia valvataeformis*
sinjana, Hauffenia jadertina—Kuščer, 1933a	"*Hauffenia*" *sinjana*
sketi, Dalmatella—Velkovrh, 1970	*Dalmatella sketi*
sketi, Hadziella—Bole, 1961	*Hadziella sketi*
*sokolovi**, *Horatia*—Starobogatov, 1962	"*Horatia*" *sokolovi**
solitaria, Hauffenia—Bole & Velkovrh, 1986	*nomen nudum*
spirata, Hauffenia minuta—Bernasconi, 1985	*Islamia spirata*
spiridoni, Bracenica—Radoman, 1973a	*Bracenica spiridoni*
st. naumi [*sic*], *Pseudamnicola* (*Rotondia*)—Radoman, 1964	*Ohridohauffenia sanctinaumi*

TABLE 5. (*Continued*)

Nominal taxon	Taxonomic status
st. zaumi [*sic*], *Horatia*—Radoman, 1964	*Zaumia sanctizaumi*
stankovici, Horatia (*Hauffenia*)—Hadžišče, 1959	*Ohrigocea stankovici*
stankovici, Lyhnidia—Hadžišče, 1959	*Lyhnidia stankovici*
sturmi, Paludina—Rosenhauer, 1856	"*Horatia*" *sturmi*
subcarinata, Hauffenia (*Hauffenia*)—Bole & Velkovrh, 1987	*Hauffenia subcarinata*
sublitoralis, Lyhnidia—Radoman, 1967	*Lyhnidia sublitoralis*
sublitoralis, Pseudamnicola (*Ohridohauffenia*)—Radoman, 1963a	*Ohridohauffenia sublitoralis*
subpiscinalis, Valvata (?)—Kuščer, 1932	*Hauffenia subpiscinalis*
sulcata, Sardohoratia—Manganelli, Bodon, Cianfanelli, Talenti & Giusti, 1998	*Sardohoratia sulcata*
supracarinata, Horatia—Bole & Velkovrh, 1986	*nomen nudum* (see *Hauffenia subcarinata*)
tellinii, Horatia (*Hauffenia*)—Pollonera, 1898	*Hauffenia tellinii*
thermalis, Hadziella—Bole, 1992	*Hadziella thermalis*
tovunica, Hauffenia (*Hauffenia*)—Radoman, 1978	*Hauffenia tovunica*
*trichoniana**, *Islamia*—Radoman, 1979	*Islamia trichoniana**
*troglobja**, "*Valvata*"—Bole & Velkovrh, 1986	*nomen nudum* (= *Islamia pusilla*)
turgidula, Valvata—Locard, 1889	possible junior synonym of *Islamia globulina*
*umbilicata**, *Hadziella*—Bole & Velkovrh, 1986	*nomen nudum*
valvataeformis, Horatia (*Hauffenia*)—Pollonera, 1898	junior synonym of *Hauffenia tellinii*
valvataeformis, Hydrobia—Möllendorff, 1873	*Islamia valvataeformis*
valvataeformis, Prespolitorea—Radoman, 1973a	*Prespolitorea valvataeformis*
verdica, Erythropomatiana—Radoman, 1978	junior synonym of *Hauffenia subpiscinalis*
verlikana, Horatia—Bourguignat, 1887	junior synonym of *Horatia klecakiana*
wagneri, Valvata—Kuščer, 1928	*Hauffenia wagneri*
wienerwaldensis, Hauffenia—Haase, 1992	*Hauffenia wienerwaldensis*
zermanica, Islamia—Radoman, 1973a	*Islamia zermanica*

species appears to have a distal (or RS1) seminal receptacle (Boeters, 1988: 220, figs. 162, 174). A distinct genus may have to be introduced for each of these species. However, we postpone this course of action until more anatomical detail is available.

An even greater number of species was assigned (sometimes tentatively) to *Neohoratia* by Boeters (1988), Boeters & Rolan (1988), Rolan (1997a, b), and Hinz et al. (1994): *N. ateni* (Boeters, 1969), *N. azarum* Boeters & Rolan, 1988; *N.* (?) *coronadoi* (Bourguignat, 1870); *N.* (?) *fezi* (Altimira, 1960); *N.* (?) *gasulli* (Boeters, 1981); *N. globulus* (Bofill, 1909) (with two subspecies: *N. g. globulus* and *N. g. lagari* (Altimira, 1960)); and *N. schuelei* (Boeters, 1981). None of these appear to belong to *Hauffenia,* as herein redefined.

"*Neohoratia*" *gasulli* was more recently revised by Ramos et al. (1992) on topotypical material. It is peculiar in that it has a large pear-shaped bursa copulatrix and is completely devoid of distinct seminal receptacles (according to Ramos et al., 1992, the function of seminal receptacles is supplied by the distal portion of the renal oviduct which is enlarged and refringent, as if it contained oriented spermatozoa); the penis has a lobe. Also in this case, we think a distinct genus will probably have to be introduced.

Anatomical study of some other species ("*N.*" *ateni,* "*N.*" *g. globulus* and "*N.*" *g. lagari;* Figs. 189–208), showed that: the female genitalia are characterized by the absence of a bursa copulatrix and the presence of two rather relatively separated seminal receptacles, the proximal larger than the distal one (Figs. 194, 200, 206); the penis is characterized by the presence of a large lobe on the left side containing a refringent mass of glandular cells; the penial duct runs inside the right side; an evident muscular pleat on ventral side, a glandular mass inside penis tip and a stylet-like structure at the opening of the penial duct are absent. Apart from the pecullar shell shape, amnicoliform or even bythinelliform (e.g., *N. ateni*), the anatomical characters distinguish these three taxa from those included in *Hauffenia.* They suggest that "*N.*" *ateni,* "*N.*" *g. globulus* and "*N.*" *g. lagari* belong to a group of *Islamia,* close to that including the

TABLE 6. Geographical distribution of valvatiform hydrobiid species from Europe and the Middle East (* taxa not discussed in the paper). The names of the countries are in parentheses when a species is present only in one or a few localities or areas of that country.

Taxa	Distribution
Arganiella pescei Giusti & Pezzoli, 1980	Latium, Marche and Abruzzo (Italy)
Bracenica spiridoni Radoman, 1973a	Montenegro
Dabriana bosniaca Radoman, 1974	Bosnia-Herzegovina
Dalmatella sketi Velkovrh, 1970	Dalmatia (Croatia)
Daphniola exigua exigua (Schmidt, 1856)	Thessalia and Peloponnesus (Greece)
"*Daphniola*" *exigua pangaea* (Reischütz, 1984)	East Makedonia (Greece)
*Daudebardiella asiana** Boettger, 1905	Turkey
*Daudebardiella naegelei** Boettger, 1905	Turkey
Fissuria boui Boeters, 1981	Vaucluse, Bouches du Rhône, Var and Alpes Maritimes (France)
Fissuria raehlei (Schütt, 1980)	Cephalonia and Zante (Greece)
"*Fissuria*" *planospira** Bodon et al., 1997	Tuscany (Italy)
Gocea ohridana Hadžišče, 1956	Lake Ohrid
Hadziella anti Schütt, 1960	Rab Island (Croatia), Slovenia and Friuli (Italy)
Hadziella deminuta Bole, 1961	Friuli-Venetia Julia (Italy) and Slovenia
Hadziella ephippiostoma Kuščer, 1932	Slovenia
Hadziella krkae Bole, 1992	Slovenia
Hadziella rudnicae Bole, 1992	Croatia
Hadziella sketi Bole, 1961	Croatia
Hadziella thermalis Bole, 1992	Slovenia and Croatia
Hauffenia danubialis (Haase, 1993)	Niederösterreich (Austria)
Hauffenia erythropomatia (Hauffen, 1856)	Slovenia
Hauffenia kerschneri (Zimmermann, 1930)	Oberösterreich and Niederösterreich (Austria)
Hauffenia media Bole, 1961	Slovenia and Croatia
Hauffenia subcarinata Bole & Velkovrh, 1987	Slovenia
Hauffenia subpiscinalis (Kuščer, 1932)	Friuli-Venetia Julia (Italy) and Slovenia
Hauffenia tellinii (Pollonera, 1898)	Eastern Venetia, Friuli-Venetia Julia (Italy) and Slovenia
Hauffenia tovunica Radoman, 1978	Croatia
Hauffenia wagneri (Kuščer, 1928)	Slovenia
Hauffenia wienerwaldensis Haase, 1992	Niederösterreich (Austria)
"*Hauffenia*" *edlaueri* (Schütt, 1961b)	Dalmatia
"*Hauffenia*" *hadei* (Gittenberger, 1982)	Lakonia, Peloponnesus (Greece)
"*Hauffenia*" *jadertina* Kuščer, 1933a	Dalmatia (Croatia)
"*Hauffenia*" *lucidula* (Angelov, 1967)	Bulgaria
"*Hauffenia*" *plana* Bole, 1961	Montenegro
"*Hauffenia*" *siniana* Kuščer, 1933a	Dalmatia (Croatia)
Heraultia exilis (Paladilhe, 1867)	Hérault (France)
Horatia klecakiana Bourguignat, 1887	Dalmatia (Croatia) and Bosnia-Herzegovina, Albania (?)
Horatia macedonica (Kuščer, 1936)	Macedonia
Horatia novoselensis Radoman, 1966	Macedonia
"*Horatia*" *birsteini** Starobogatov, 1962	Caucasus
"*Horatia*" *borutzkii** Zhadin, 1932	Caucasus
"*Horatia*" *gasulli* (Boeters, 1981)	East Spain
"*Horatia*" *gatoa* Boeters, 1980	South Spain
"*Horatia*" *knorr** Schütt, 1961	Dalmatia
"*Horatia*" *ljovuschkini** Starobogatov, 1962	Caucasus
"*Horatia*" *parvula** (Naegele, 1894)	Turkey
"*Horatia*" *sokolovi** Starobogatov, 1962	Caucasus
"*Horatia*" *stumi* (Rosenhauer, 1856)	South Spain
*Islamia anatolica** Radoman, 1973a	Turkey
Islamia ateni (Boeters, 1969)	Northeast Spain
Islamia azarum (Boeters & Rolan, 1988)	Northwest Spain
*Islamia bosniaca** Radoman, 1973a	Bosnia-Herzegovina
*Islamia burnabasa** (Schütt, 1964)	Turkey
Islamia cianensis Bodon et al., 1995	Sicily (Italy)
Islamia consolationis (Bernasconi, 1985)	Doubs (France)

TABLE 6. (*Continued*)

Taxa	Distribution
Islamia gaillardoti (Germain, 1911)	Israel
Islamia gaiteri Bodon et al., 1995	Elba Island (Italy)
Islamia globulina (Paladilhe, 1866)	South and East France
Islamia globulus globulus (Bofill, 1909)	Northeast Spain
Islamia globulus lagari (Altimira, 1960)	Northeast Spain
*Islamia graeca** Radoman, 1973a	Amvrakia Lake, Etolia (Greece)
*Islamia latina** Radoman, 1973a	Dalmatia (Croatia)
Islamia mienisi (Schütt, 1991)	Israel and Lebanon
Islamia minuta (Draparnaud, 1805)	Doubs, Jura and Ain (France), Neuchâtel (Switzerland)
*Islamia pseudorientalica** Radoman, 1973a	Turkey
*Islamia pusilla** (Piersanti, 1952)	Campania, Abruzzo and Apulia (Italy)
Islamia schuelei (Boeters, 1981)	South Spain
Islamia spirata (Bernasconi, 1985)	Doubs (France)
*Islamia trichoniana** Radoman, 1979	Trichonis Lake, Etolia (Greece)
Islamia valvataeformis (Möllendorff, 1873)	Bosnia-Herzegovina
Islamia zermanica Radoman, 1973a	Croatia
"*Islamia*" *bendidis** Reischütz, 1988	Samothraki Island (Greece)
"*Islamia*" *coronadoi* (Bourguignat, 1870)	Central Spain
"*Islamia*" *epirana* (Schütt, 1962)	Ipiros, Etolia and Lefkada (Greece)
"*Islamia*" *fezi* (Altimira, 1960)	East Spain
Karevia omata (Radoman, 1957)	Lake Ohrid
Kerkia brezicensis Bodon & Cianfanelli, 1996	Slovenia
Kerkia kusceri (Bole, 1961)	Slovenia
Lyhnidia giorgievici Hadžišče, 1959	Sweti Naum Lake, Ohrid basin
Lyhnidia hadzii Hadžišče, 1959	Lake Ohrid
Lyhnidia karamani Hadžišče, 1959	Lake Ohrid
Lyhnidia stankovici Hadžišče, 1959	Lake Ohrid
Lyhnidia sublitoralis Radoman, 1967	Lake Ohrid
Ohridohauffenia depressa (Radoman, 1957)	Lake Ohrid
Ohridohauffenia drimica (Radoman, 1964)	Ohrid basin
Ohridohauffenia minuta (Radoman, 1955)	Ohrid basin
Ohridohauffenia rotonda (Radoman, 1964)	Lake Ohrid
Ohridohauffenia sanctinaumi (Radoman, 1964)	Ohrid basin
Ohridohauffenia sublitoralis (Radoman, 1963a)	Lake Ohrid
Ohrigocea karevi Hadžišče, 1959	Lake Ohrid
Ohrigocea miladinovorum Hadžišče, 1959	Lake Ohrid
Ohrigocea samuili Hadžišče, 1959	Lake Ohrid
Ohrigocea stankovici (Hadžišče, 1959)	Lake Ohrid and Ohrid basin
Pezzolia radapalladis Bodon & Giusti, 1986	Liguria (Italy)
Prespolitorea malaprespensis Radoman, 1973a	Mirka Prespa Lake (Albania)
Prespolitorea valvataeformis Radoman, 1973a	Prespa Lake
Pseudohoratia brusinae (Radoman, 1953)	Lake Ohrid
Pseudohoratia lacustris (Radoman, 1964)	Lake Ohrid
Pseudohoratia ochridana (Polinski, 1929)	Lake Ohrid
Pseudoislamia balcanica Radoman, 1979	Trichonis Lake Etolia (Greece)
Sardohoratia islamioides Manganelli et al., 1998	Sardinia Island (Italy)
Sardohoratia sulcata Manganelli et al., 1998	Sardinia Island (Italy)
*Sheitanok amidicus** Schütt & Sesen, 1991	Turkey
Strugia ohridana Radoman, 1973a	Ohrid basin
Zaumia kusceri (Hadžišče, 1959)	Ohrid basin
Zaumia sanctizaumi (Radoman, 1964)	Lake Ohrid

French "*Hauffenia*" species (see the redescription of the French *Islamia* in "Descriptions of some taxa misidentified as *Hauffenia* species").

North American Species. Two valvatiform species from North America, *Valvata micra* Pilsbry & Ferris, 1906, and *Valvata micra nugax* Pilsbry & Ferris, 1906, were assigned to *Hauffenia* by Bole & Velkovrh (1986) and to *Hauffenia* and *Horatia* respectively by Burch (1989). An anatomical revision by Hershler & Longley (1986) in the same years showed that these species belong to a distinct, North

TABLE 7. Analytical key for identification of the *Hauffenia* species (only species certainly belonging to *Hauffenia* are considered). For characters used, see Fig. 188.

1a — Operculum with peg, from small to very well developed	2
1b — Operculum without peg or, all the most, with very reduced peg	7
2a — Peg small, not dilated at the top	3
2b — Peg well developed, dilated at the top	5
3a — Shell with spire moderately to well raised; penis with one wide lateral lobe	*H. wagneri*
3b — Shell with spire slightly raised	4
4a — Penis with one lateral lobe poorly developed; intestine with bend tightly coiled on pallial wall	*H. media*
4b — Penis with one wide lateral lobe; intestine with bend slightly coiled on pallial wall	*H. kerschneri*
5a — Peg of medium size; penis without or with slightly evident lobe/s	6
5b — Peg very well developed: penis with one rather evident lateral lobe	*H. tovunica*
6a — Shell with a keel on the lower wall of the last whorl around umbilicus	*H. subcarinata*
6b — Shell not keeled	*H. tellinii*
7a — Penis with 1–3 small lateral lobes; no peg	8
7b — Penis without lobes	9
8a — Shell with spire well raised; diameter 1.4–2.9 mm	*H. subpiscinalis*
8b — Shell with spire rather flat; diameter 1.17–1.55 mm	*H. erythropomatia*
9a — No peg	*H. danubialis*
9b — Peg very reduced	*H. wienerwaldensis*

American genus, *Phreatodrobia* Hershler & Longley, 1986.

THE SPECIES OF HAUFFENIA

Hauffenia danubialis (Haase, 1993)

Lobaunia danubialis Haase, 1993: 99–105, figs. 8B, 9–15.

Type Locality and Type Material: see *Lobaunia danubialis* Haase, 1993, in the section on the taxa of the genus group.

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform-planispiral, with spire almost flat; operculum without peg; penis without lobes.

Material Examined and Description

See *Lobaunia danubialis* Haase, 1993, in the section on the taxa of the genus group.

Distribution

Niederösterreich, Austria.

Taxonomy

Hauffenia danubialis was assigned to a distinct genus, *Lobaunia,* by Haase (1993). This genus is here regarded as a junior synonym of *Hauffenia*. It is distinct from *H. wienerwaldensis,* due to complete absence of an opercular peg.

Hauffenia erythropomatia (Hauffen, 1856)

Valvata erythropomatia Hauffen, 1856: 465.

Type Locality and Type Material: see *Erythropomatiana erythropomatia* (Hauffen, 1856) in the section devoted to the taxa of the genus group.

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform, with spire rather flat; operculum without peg; penis with 2–3 small lateral lobes.

Material Examined and Description

See *Erythropomatiana erythropomatia* (Hauffen, 1856) in the section devoted to the taxa of the genus group.

Distribution

North of Ljubljana, Slovenia.

Taxonomy

Hauffenia erythropomatia was assigned to a distinct genus, *Erythropomatiana,* by Rado-

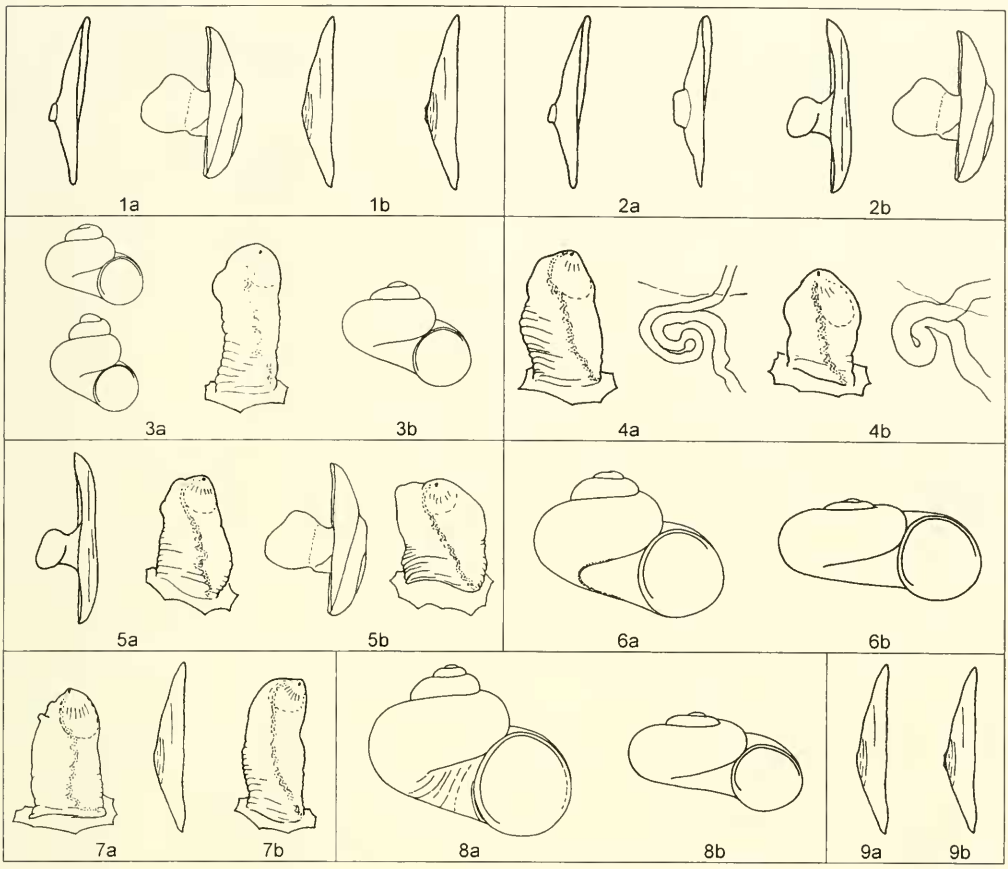


FIG. 188. Characters used in the analytical key for the identification of the *Hauffenia* species (Table 7).

man (1978). This genus is here regarded as a junior synonym of *Hauffenia*.

***Hauffenia kerschneri* (Zimmermann, 1930)**

Horatia erythropomatia kerschneri Zimmermann, 1930: 233–234, pl. 13, figs. 3–6.

Type Locality: ". . . in den zuführenden Quellkanälen der Wasserleitung in Weyer an der Enns (Oberösterreich)", Austria.

Type Material: lectotype (NHMW 85034) and 19 paralectotypes (NHMW K 48844) at the Naturhistorisches Museum Wien, Vienna, Austria (Haase, 1993).

Hauffenia kerschneri loichiana Haase, 1993: 94–98.

Type Locality: "Kleine Quelle unterhalb des Fuchslochs (Höhlenkatastern. 1837/24) bei Loich im westlichen Niederösterreich (Seitental der Pielach)", Austria.

Type Material: holotype (NHMW 85029) and 68 paratypes (NHMW 85030, shells) at the Naturhistorisches Museum Wien, Vienna, Austria (Haase, 1993).

Diagnosis

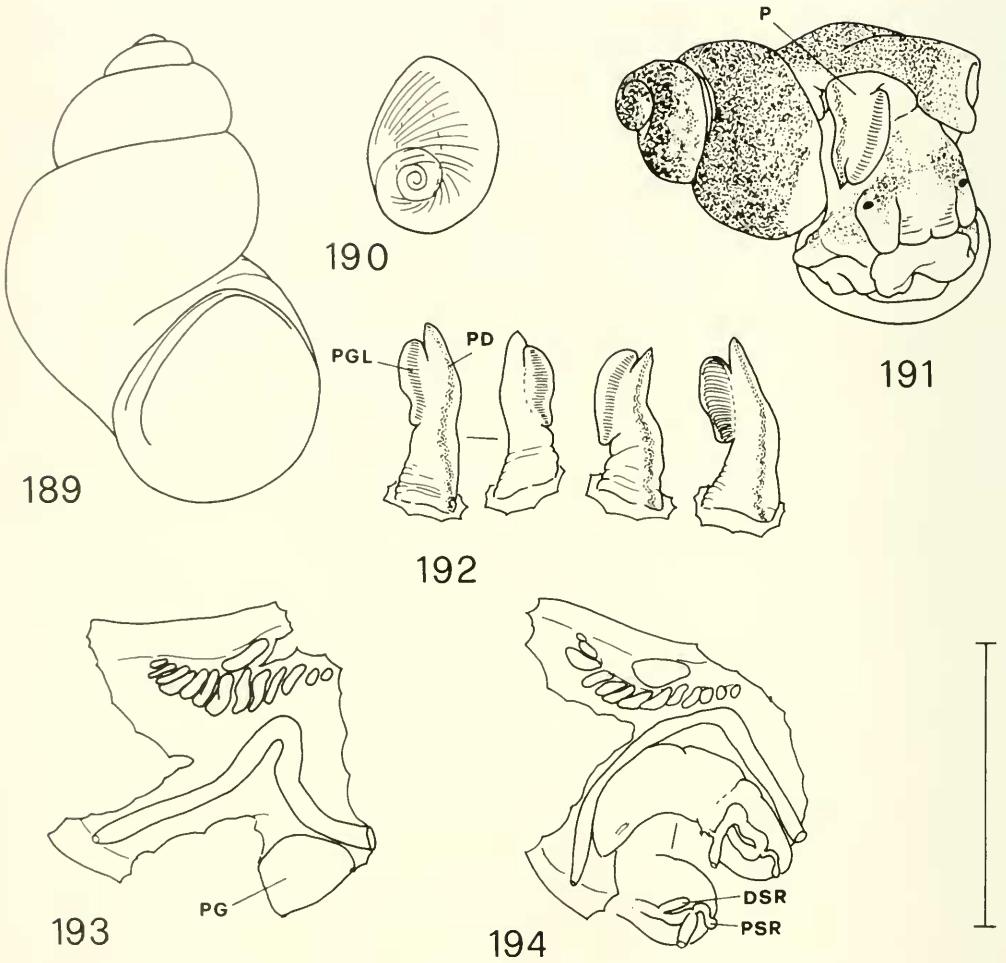
A species of *Hauffenia* having shell very small, valvatiform, with spire not very raised; operculum with small peg; penis with one wide lateral lobe.

Material Examined

– Spring in Weyer an der Enns (type locality), Oberösterreich, Austria, M. Bodon leg. 10.6.1985 (3 males, 3 females, many shells).

Description

Shell very small, valvatiform, thin, waxen, transparent when fresh; surface of protoconch malleated; spire not very raised, con-



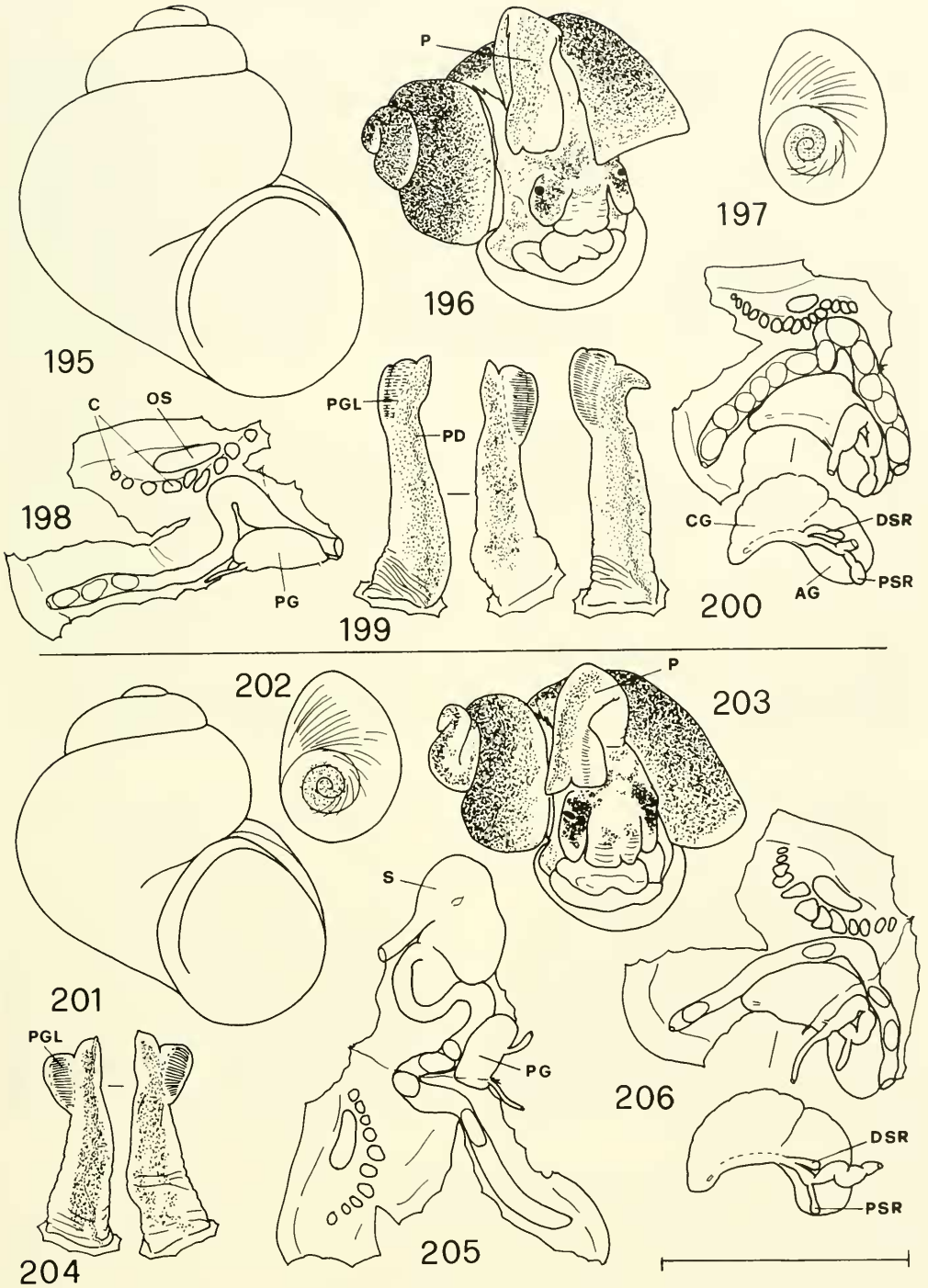
FIGS. 189–194. Shell, operculum and anatomical details of *Islamia ateni* (Boeters, 1969) from the thermal spring at Banys de Sant Vicienç, Cataluña, Spain, M. Bodon leg. 14.9.1985. Fig. 189: shell; Fig. 190: outer face of operculum; Fig. 191: body of a male with pallial cavity open to show head and penis; Fig. 192: dorsal side and ventral side (second picture) of penis of three males; Fig. 193: prostate gland, intestine and pallial organs of a male; Fig. 194: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

sisting of 2.5–3.25 rather rapidly growing convex whorls; last whorl large, dilated, descending slightly near aperture; umbilicus wide; aperture prosocline, oval; peristome complete, thin, slightly thickened, slightly reflected only at columellar margin (Figs. 214, 215; Zimmermann, 1930: 233–234, pl. 13, figs. 3–6; Haase, 1993: 92, fig. 1A–D, table 1, as *Hauffenia k. kerschneri;* Haase, 1993: 94, fig. 4A–D, table 1, as *H. k. loichiana;* Boeters, 1998: 28, fig. H6). Dimensions : height = 0.70–1.09 mm; diameter = 1.00–1.61 mm.

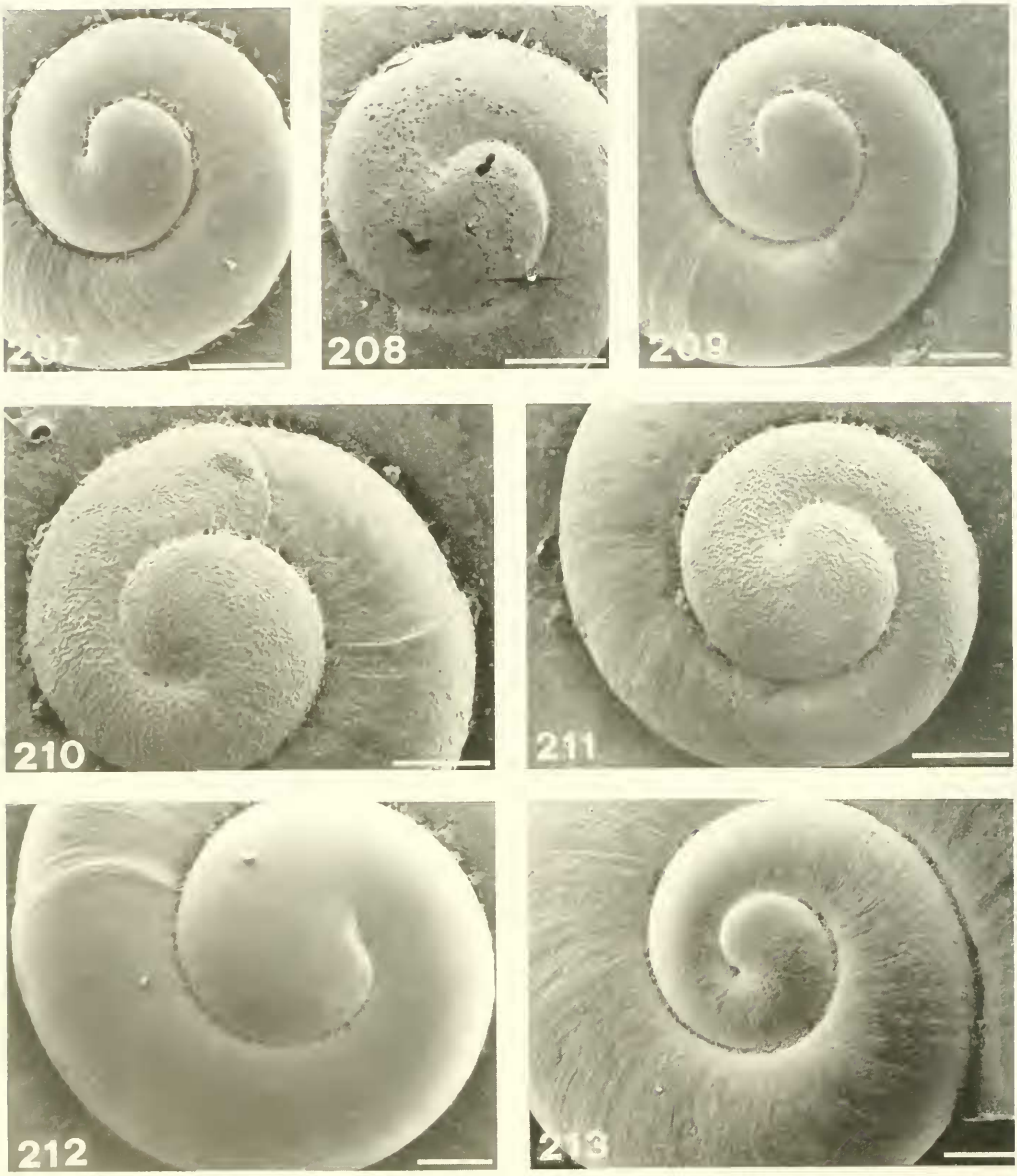
Operculum thin, orange, paucispiral, with small spiralized peg at centre of inner face (Fig. 216; Haase, 1993: 92, fig. 2A, B, as *Hauffenia k. kerschneri;* Haase, 1993: 94, as *H. k. loichiana*).

Body unpigmented (a few black spots on visceral sac); eye spots absent (Fig. 217; Haase, 1993: 94, as *H. k. loichiana*).

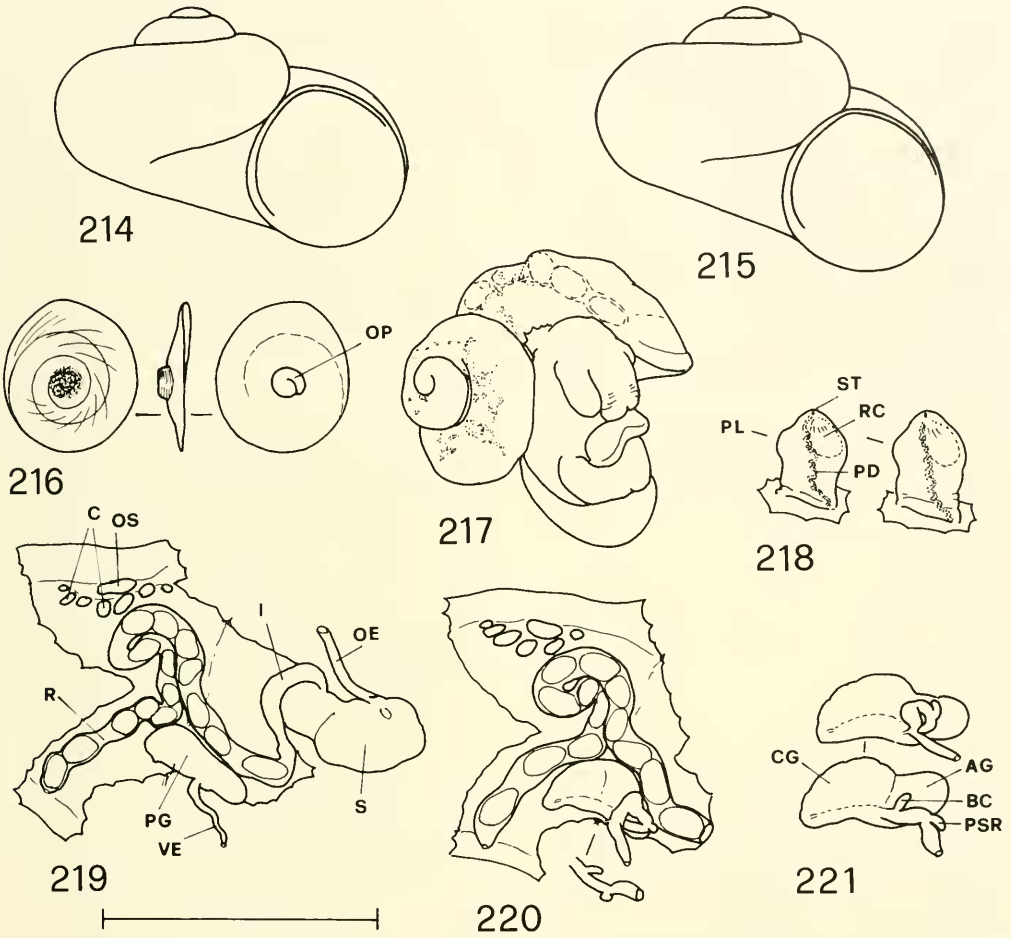
Male genitalia with prostate gland bulging well into pallial cavity; penis short, flat, with apex blunt, and one lateral, not very raised but wide lobe on left side; penial duct zig-zagging through central portion of penis to open at penis tip; globular mass of refringent cells



FIGS. 195–206. Shell, operculum and anatomical details of *Islamia globulus globulus* (Bofill, 1909) from the spring near Guardiola, Cataluña, Spain, M. Bodon leg. 14.9.1985 (Figs. 195–200) and of *Islamia globulus lagari* (Altimira, 1960) from the spring Fuente Les Dous, Torrelles de Foix, Cataluña, Spain, M. Bodon leg. 2.1.1992 (Figs. 201–206). Figs. 195, 201: shells; Figs. 196, 203: body of a male with pallial cavity open to show head and penis; Figs. 197, 202: outer face of operculum; Figs. 198, 205: prostate gland, stomach (excluded in Fig. 198), intestine and pallial organs of a male; Figs. 199, 204: dorsal and ventral side (second picture) of penis; Figs. 200, 206: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.



FIGS. 207–213. Microsculpture of protoconchs. Fig. 207: *Islamia ateni* (Boeters, 1969) from the thermal spring at Banys de Sant Vicienç, Cataluña, Spain, M. Bodon leg. 14.9.1985; Fig. 208: *Islamia globulus globulus* (Bofill, 1909) from the spring near Guardiola, Cataluña, Spain, M. Bodon leg. 14.9.1985; Fig. 209: *Islamia minuta* (Draparnaud, 1805) from the Source de l'Ain, Nozeroy, Jura, France, M. Bodon leg. 21.7.1985; Fig. 210: *Islamia globulina* (Paladilhe, 1866) from the Rivière souterraine de Labouiche, Foix, Ariège, France, M. Bodon leg. 13.9.1985; Fig. 211: *Islamia spirata* (Bernasconi, 1985) from the stream near Pont les Moulins, Cusancin valley, Doubs, France, M. Bodon leg. 22.7.1985; Fig. 212: *Islamia consolationis* (Bernasconi, 1985) from the springs at Consolation-Maisonnettes, Doubs, France, M. Bodon & G. Manganelli leg. 13.6.1996; Fig. 213: *Heraultia exilis* (Paladilhe, 1867) from the Source du Lez, Hérault, France, M. Bodon leg. 2.12.84. Scale bar = 100 μm.



FIGS. 214–221. Shell, operculum and anatomical details of *Hauffenia kerschneri* (Zimmermann, 1930) from the spring in Weyer an der Enns, Oberösterreich, Austria, M. Bodon leg. 10.6.1985. Figs. 214, 215: shells; Fig. 216: outer face (left), profile (centre) and inner face (right) of operculum; Fig. 217: body of a female with pallial cavity open to show head; Fig. 218: dorsal side of penis of two males; Fig. 219: prostate gland, stomach, intestine and pallial organs of a male; Fig. 220: renal and pallial oviduct, intestine and pallial organs of a female; Fig. 221: renal and pallial oviduct of a female. Scale bar = 1 mm.

inside penis apex to right of penial duct (no data about this in Haase, 1993); terminal part of penial duct (immediately before opening) with very small stylet (Figs. 218, 219; Haase, 1993: 95–96, 98, figs. 5, 7, 8, as *H. k. loichiana;* Boeters, 1998: 28, fig. H7).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle very small, with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, about same size as seminal receptacle, slightly dilated at apex, arising very close to where oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Figs. 220, 221; Haase, 1993: 95, 98, figs. 5, 6, as *Hauffenia k. loichiana;* Boeters, 1998: 28, fig. H8).

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5 smaller denticles on both sides, in decreasing order of size; 2 basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elon-

gated cutting edge with long row of 21–22 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 13–15 very small denticles (Haase, 1993: 92, fig. 3A, B, as *H. k. kerschneri;* Haase, 1993: 94, fig. 3C, D, as *H. k. loichiana*).

Stomach without posterior caecum; intestine with well developed, S-like bend on pallial wall (Figs. 219, 220; Haase, 1993: 95, fig. 5, as *H. k. loichiana*).

Osphradium variable in size, elliptical or kidney-shaped; ctenidium consisting of 6–9 lamellae (Figs. 219, 220; Haase, 1993: 94, as *H. k. loichiana*).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Haase, 1993: 95, as *H. k. loichiana*).

Distribution

Oberösterreich and Niederösterreich, Austria.

Taxonomy

The small opercular peg and the penis with wide penial lobe suggest relationships with *Hauffenia wagneri* (Kuščer, 1928) or *H. media* Bole, 1961. Nevertheless, due to other weak anatomical characters (intestine with less tightly coiled bend on pallial wall) and the distance between the type localities and the distributions of these species, we prefer to maintain *H. kerschneri* as a distinct species.

Haase (1993) divided the species into two subspecies on the basis of an unique difference in the shell morphometry of a single population; this is not significant considering the marked variability in shell dimensions of the single populations of *Hauffenia* species.

Hauffenia media Bole, 1961

Hauffenia media Bole, 1961: 62–63, 67–68, fig. 3B.

Type Locality: "jama Vrlovka pri Kamanju ob Kolpi", Croatia.

Type Material: Bole (1961) did not give any information about the type material.

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform, with spire slightly raised; operculum with very small peg; penis with one wide but not very raised lateral lobe.

Material Examined

– Spring near Kostanjevica, Krško, Slovenia, 33T WL 37, A. Edlauer leg., (Naturhistorisches Museum Wien no. 21418; 1 shell with operculum, 3 shells, determined by H. Schütt).
– "Kostanjeviška Jama" cave, S. 518, Kostanjevica, Krško, Slovenia, 33T WL 37, F. Stoch leg. 16.6.1996 (1 female).

Description

Shell very small, valvatiform, thin, waxen, transparent when fresh; surface of protoconch malleated; spire slightly raised, consisting of 3–3.25 rather rapidly growing convex whorls; last whorl large, dilated, descending slightly near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, thin, slightly reflected only at columellar margin (Figs. 222–224; Bole, 1961: 62–63, 67, fig. 3B). Dimensions: height = 1.0–1.2 mm; diameter = 1.4–1.9 mm (Bole, 1961).

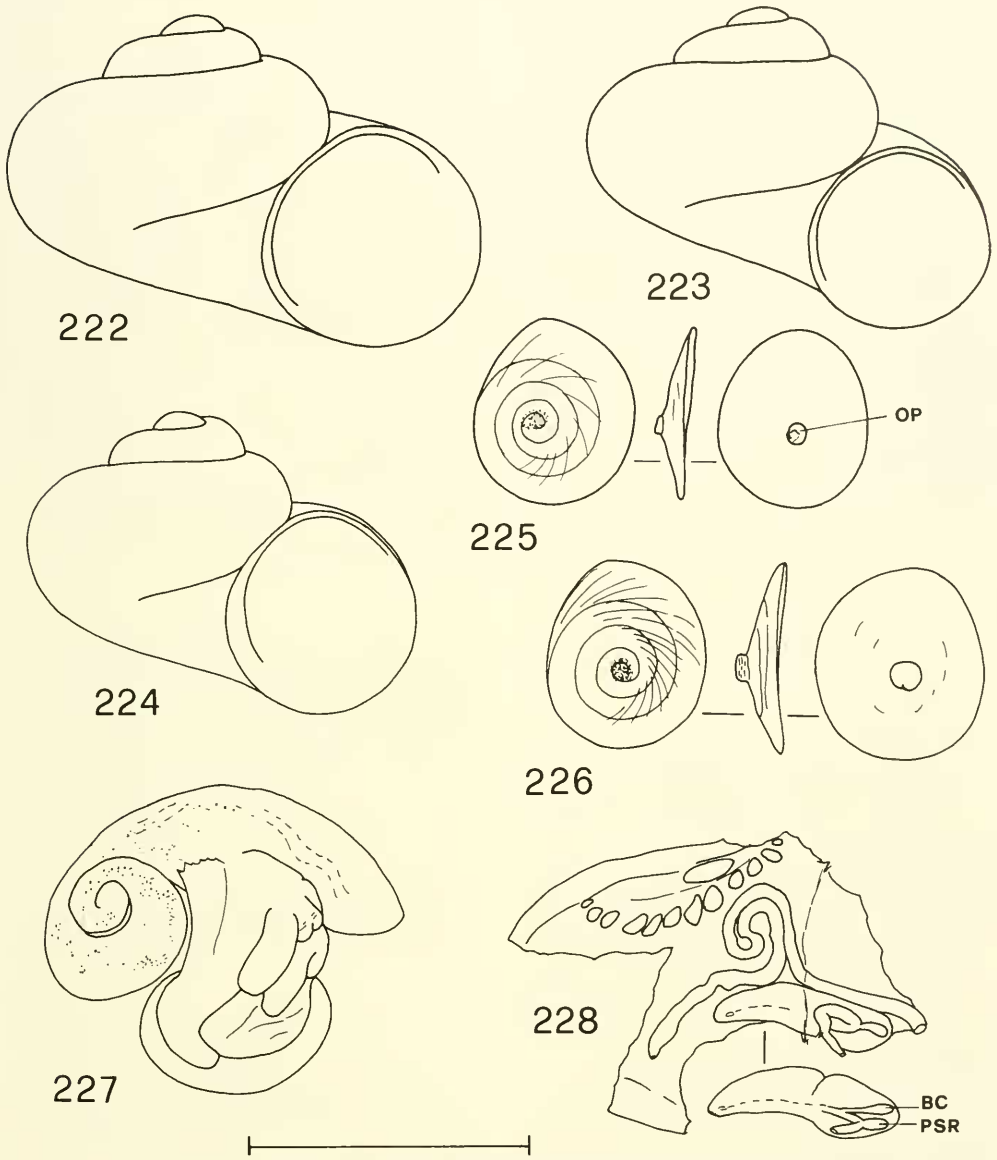
Operculum thin, paucispiral, yellowish, with very small spiralized peg at centre of inner face (Figs. 225, 226; Bole, 1961, 62, 67, fig. 3B; 1993: 6).

Body unpigmented (a few traces of pigment in wall of visceral sac); eye spots absent (Fig. 227).

Male genitalia with penis rather elongated, flat, with apex blunt, slightly pointed at centre and one wide, but not very raised lateral lobe on left side; penial duct zig-zagging through sub-central portion of penis to open at penis tip; no data available about existence of globular mass of refringent cells inside penis apex to right of penial duct and of stylet (Bole, 1961: 62, 67, fig. 3B).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle small, with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, a little longer than seminal receptacle, slightly dilated at apex, arising very close to where oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Fig. 228).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle



FIGS. 222–228. Shell, operculum and anatomical details of *Hauffenia media* Bole, 1961, from the spring near Kostanjevica, Krško, Slovenia, A. Edlauer leg., (Naturhistorisches Museum Wien no. 21418) (Figs. 222, 223, 225) and from the "Kostanjeviška Jama" cave, S. 518, Kostanjevica, Krško, Slovenia, F. Stoch leg. 16.6.1996 (Figs. 224, 226–228). Figs. 222–224: shells; Figs. 225, 226: outer face (left), profile (centre) and inner face (right) of operculum; Fig. 227: body of a female with pallial cavity open to show head; Fig. 228: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

and 4–5 smaller denticles on both sides in decreasing order of size; one basal cusp where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10 denticles, central one longer, larger; first marginal teeth with apical row of 23–28 denticles; second marginal teeth with apical row of 18–24 denticles (Bole, 1961: 62, 67, fig. 3B).

Stomach without posterior caecum; intestine with well-developed, tightly coiled, S-like bend on pallial wall (Fig. 228).

Osphradium elongated; ctenidium consisting of 8–12 lamellae (Fig. 228; Bole, 1961: 62, 67).

Nervous system unknown.

Distribution

Eastern Slovenia and northern Croatia.

Taxonomy

The anatomical data is not complete enough to draw conclusions on the status of this species. Penis shape, female genitalia and operculum structure are sufficient to infer it belongs to *Hauffenia*. The small opercular peg suggests relationships with *H. wagneri* (Kuščer, 1928).

Hauffenia subcarinata Bole & Velkovrh, 1987

Horatia supracarinata Bole & Velkovrh, 1986: 193, *nomen nudum.*

Hauffenia (*Hauffenia*) *subcarinata* Bole & Velkovrh, 1987: 72–73, 78–79, fig. 1A–C, pl. 1, figs. 1, 2.

Type Locality: "Izvir v vasi Ložice pri Desklah v dolini Soče. 12 km severno severozahodno od Nove Gorice/Quelle im Dorf Ložice bei Deskle in Soča-Tal, 12 km NNW von Gorica", Slovenia.

Type Material: holotype (35215a) in the Velkovrh collection, Biotehniška fakulteta Univerza Edvarda Kardelja, Ljubljana, Slovenia, together with paratypes (35215/80) (Bole & Velkovrh, 1987).

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform, with spire moderately raised; lower wall of last whorl with keel; operculum with well-developed peg; penis without lobes.

Material Examined

– Spring near Ložice, along road to Kanal, Soča valley, Slovenia, 33T UM 9201, M. Bodon leg. 10.7.1996 (1 shell with operculum, many shells) (type locality).

– Spring in camping area at Kanal, Soča valley, Slovenia, 33T UM 9404, S. Cianfanelli & M. Calcagno leg. 31.7.1994 (1 shell with operculum, 5 shells).

Description

Shell very small, valvatiform, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire moderately raised, conical, consisting of 2.75–3.5 rather rapidly growing convex whorls; last whorl large, dilated, descending slightly near aperture, its lower wall (around umbilicus) having keel ending at aperture; umbilicus wide; aperture prosocline, oval, slightly angled at lower margin (near keel); peristome complete, thin, slightly thickened, slightly reflected only at lower and columellar margin (Figs. 94, 229; Bole & Velkovrh, 1987: 72, 78, pl. 1, figs. 1, 2; Bole, 1993: 6). Dimensions: height = 0.83–1.30 mm; diameter = 1.14–1.90 mm (Bole & Velkovrh, 1987).

Operculum thick, yellowish brown, paucispiral, with well-developed, spiralized peg at centre of inner face (Fig. 230; Bole, & Velkovrh, 1987: 72, 79, fig. 1B, C; Bole, 1993: 6).

Body unpigmented; eye spots absent.

Male genitalia with penis rather elongated, cylindrical, flat, slightly tapering near apex, ending in a slightly blunt tip, without penial lobes; penial duct zig-zagging through central portion of penis to open at penis tip; no data available about existence of globular mass of refringent cells inside penis apex to right of penial duct and of stylet (Bole & Velkovrh, 1987: 72, 79, fig. 1A; Bole, 1993: 6).

Female genitalia unknown.

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 4 smaller denticles on both sides in decreasing order of size; two basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 18–20 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 14–16 very small denticles (Bole & Velkovrh, 1987: 72, 79, fig. 1C; Bole, 1993: 6).

Stomach, intestine, osphradium, ctenidium and nervous system unknown.

Distribution

Soča [Isonzo] valley, western Slovenia.

Taxonomy

Penis characters and operculum with peg are probably sufficient to justify inclusion of this species in the genus *Hauffenia.*

Hauffenia subpiscinalis (Kuščer, 1932)

Valvata (?) *subpiscinalis* Kuščer, 1932: 51–53, pl. 5, fig. 1.

Type Locality and Type Material: see *Neohoratia subpiscinalis* (Kuščer, 1932) in the section devoted to the taxa of the genus group.

Erythropomatiana verdica Radoman, 1978: 36, pl. 5, figs. 20, 21.

Type Locality and Type Material: see the synonymy of *Neohoratia subpiscinalis* (Kuščer, 1932) in the section devoted to the taxa of the genus group.

Diagnosis

A species of *Hauffenia* having shell very small but larger than the other species of the genus, valvatiform, with spire well raised; operculum without peg; penis with 1–3 small lateral lobes.

Material Examined and Description

See *Neohoratia subpiscinalis* (Kuščer, 1932) in the section devoted to the taxa of the genus group.

Distribution

Eastern Friuli-Venetia Julia, Italy, and Western Slovenia, from Soča [Isonzo] valley to Ljubljana area.

Taxonomy

Hauffenia subpiscinalis was recently assigned to a distinct genus, *Neohoratia,* by Bole & Velkovrh (1986), Boeters (1988), and Bole (1993). This genus is here regarded as a junior synonym of *Hauffenia.*

Erythropomatiana verdica Radoman, 1978, is here recognized as a junior synonym of *H. subpiscinalis.* Radoman (1978) distinguished *H. verdica* from *H. subpiscinalis* on the basis of few differences (penis shape; slightly larger bursa copulatrix), deduced from the drawings of *H. subpiscinalis* published by Bole (1967: fig. 3A). It is true that Bole showed a squatter penis with larger lobes than those figured by Radoman (1978: fig. 6) in *H. erythropomatia,* but as we verified with topotypical specimens, *E. verdica* also has a squat penis (Fig. 130). *Hauffenia subpiscinalis* from the typical area showed penis lobes variable in number (2–3) and shape, often very similar to those of *E. verdica* and *H. erythropomatia* (Figs. 138, 140). Regarding the bursa copulatrix, our studies on many populations not only revealed bursa size to be rather variable, but also that specimens of *H. subpiscinalis* from the typical area have a bursa proportionally larger than those figured by Bole (1967) and similar to those found in *E. verdica* from Vrhnika (Figs. 131, 135–137). Shell shape is also similar in the type species of the two genera (cf., Bole, 1970, 1979; Radoman, 1978).

Hauffenia tellinii (Pollonera, 1898)

Horatia (*Hauffenia*) *Tellinii* Pollonera, 1898: 3, 4, fig. 2.

Type Locality and Type Material: see *Hauffenia tellinii* (Pollonera, 1898) in section devoted to taxa of the genus group.

Horatia (*Hauffenia*) *valvataeformis* Pollonera, 1898: 3–4, fig. 3.

Type Locality and Type Material: see synonymy of *Hauffenia tellinii* (Pollonera, 1898) in section devoted to the taxa of the genus group.

Hauffenia michleri Kuščer, 1932: 56–57, pl. 5, fig. 3.

Type Locality and Type Material: see synonymy of *Hauffenia tellinii* (Pollonera, 1898) in section devoted to the taxa of the genus group.

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform to planispiral, with spire from rather raised to almost flat; operculum with well developed peg; penis with 1–2 slightly evident lateral lobes, sometimes absent.

Material Examined and Description

See *Hauffenia tellinii* (Pollonera, 1898) in section devoted to taxa of the genus group.

Distribution

From eastern Venetia and Friuli-Venetia Julia, Italy, to western Slovenia in the Ljubljana area.

Taxonomy

We agree with Bole (1970) about the synonymy of the two species described by Pollonera from the upper Natisone valley: *Horatia* (*Hauffenia*) *tellinii* and *H.* (*H.*) *valvataeformis*. The latter is distinguished from the former by a shell with raised spire, which is clearly only one end of a spectrum of shell shape. The two extreme morphs (spire depressed: *tellinii;* spire raised: *valvataeformis*) and their intermediates were found in many of the populations examined.

Our study does not confirm the existence of constant and valid shell, anatomical and opercular characters that justify regarding *H. michleri* as a species distinct from *H. tellinii*. Traditional distinction of the two species was evidently based on anatomical study of very few specimens. Hence, we propose *H. michleri* as a junior synonym of *H. tellinii*.

Hauffenia populations from the southeastern Karst in the province of Trieste have an operculum with a reduced peg; they were tentatively assigned to *H. tellinii* (Pezzoli, 1988a; Bodon & Giovannelli, 1993).

Hauffenia tovunica Radoman, 1978

Hauffenia (*Hauffenia*) *tovunica* Radoman, 1978: 34, fig 5A–E, pl. 4, figs. 11, 12.

Type Locality: "Die Grotte Tounjčica, neben dem Ort Tounj, in der Nähe der Strasse Duga resa—Josipdol", Croatia.

Type Material: holotype and four paratypes (SMF 249614) at the Senckenberg-Museum, Frankfurt am Main, Germany (Jovanović, 1991).

Diagnosis

A species of Hauffenia having shell very small, valvatiform, with spire not very raised; operculum with very well-developed dilated peg; penis with one rather evident lateral lobe.

Material Examined

- "Tounjčica Spilja" cave, Tounj, east of Ogulin, Croatia, E. Kletečki, F. Gasparo & F. Stoch leg. 13.7.1997 (1 male, 1 young specimen, 12 shells).

Description

Shell very small, valvatiform, not very thin, transparent when fresh; surface of protoconch malleated; spire not very raised, consisting of 3.25–3.75 rather rapidly growing convex whorls; last whorl large, dilated, slightly descending near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, somewhat thickened and reflected (Fig. 231; Radoman, 1978: 34, pl. 4, figs. 11, 12; Radoman, 1983: 122, pl. 9, fig. 142; Jovanović, 1991: pl. 8, fig. 66). Dimensions: height = 1.26–1.68 mm; diameter = 1.81–2.02 mm (Radoman, 1983: table 7).

Operculum rather thick but with thin edge, paucispiral, convex, but concave at centre, with very well-developed, dilated and spiralized peg at centre of inner face (Fig. 235; Radoman, 1978: 33–34, fig. 5D, E; Radoman, 1983: 120, fig. 67D, E).

Body unpigmented (a few black spots on visceral sac); eye spots absent (Fig. 233).

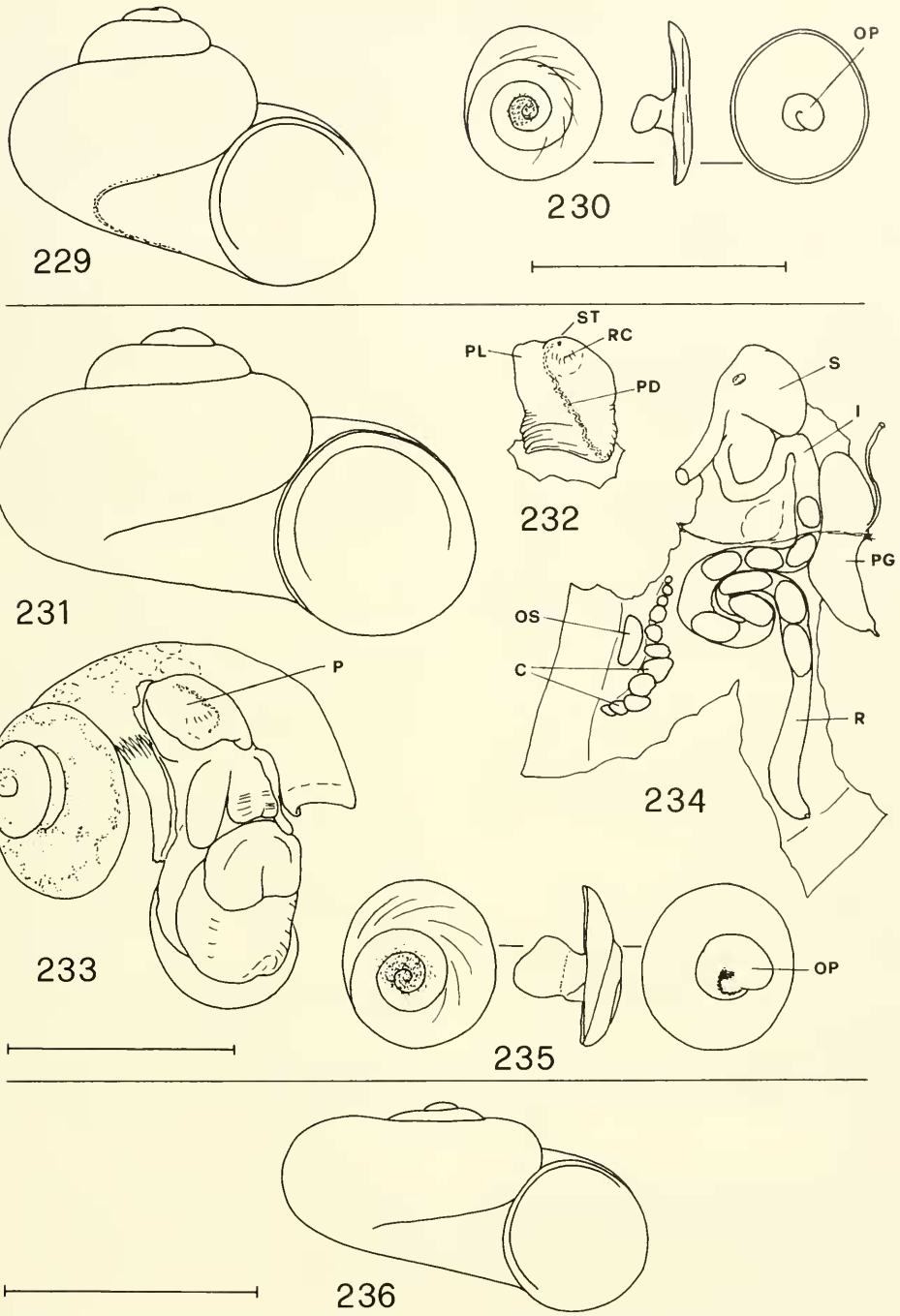
Male genitalia with prostate gland bulging well into pallial cavity; penis rather short, flat, with apex blunt, and one rather evident, knob-like, lateral lobe on left side near apex; penial duct zig-zagging through central portion of penis to open at penis tip; globular mass of refringent cells inside penis apex to right of penial duct and terminal part of penial duct with very small stylet (Fig. 232; Radoman, 1978: 33, fig. 5C; 1983: 120, fig. 67C).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle very small, with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, small but markedly longer than seminal receptacle, slightly dilated at apex, arising very close to where oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Radoman, 1978: 33, fig. 5A, B; 1983: 40, 120, fig. 67A, B).

Radula with central tooth with one pair of basal cusps; other details unknown (Radoman, 1978: 33; 1983: 114).

Stomach without posterior caecum; intestine with well-developed, tightly coiled, S-like bend on pallial wall (Fig. 234; Radoman, 1983: 40).

Osphradium kidney-shaped; ctenidium consisting of about 11 lamellae (Fig. 234).



FIGS. 229–236. Shell, operculum and anatomical details of *Hauffenia subcarinata* Bole & Velkovrh, 1987, from the spring near Ložice, along the road to Kanal, Soča valley, Slovenia, 33T UM 9201, M. Bodon leg. 10.7.1996 (Figs. 229, 230), *Hauffenia tovunica* Radoman, 1978, from the "Tounjčica Spilja" cave, Tounj, east of Ogulin, Croatia, E. Kletečki, F. Gasparo & F. Stoch leg. 13.7.1997 (Figs. 231–235) and of *Hauffenia wienerwaldensis* Haase, 1992, from the upper well in Klamm 106, Wienerwald, Niederösterreich, Austria, M. Haase leg. 17.7.1989 (Fig. 236). Figs. 229, 231, 236: shells; Figs. 230, 235: outer face (left), profile (centre) and inner face (right) of operculum; Fig. 232: dorsal side of penis; Fig. 233: body of a male with pallial cavity open to show head and penis; Fig. 234: prostate gland, stomach, intestine and pallial organs of a male. Scale bar = 1 mm.

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Radoman, 1978: 33; 1983: 120).

Distribution

Known only from the type locality, near Ogulin, northern Croatia.

Taxonomy

The study of the male genitalia confirms that the this species is distinct and that it belongs to *Hauffenia*. Compared to *H. tellinii, H. tovunica* has more developed opercular peg and penial lobe.

Hauffenia wagneri (Kuščer, 1928)

Valvata wagneri Kuščer, 1928: 50, fig. 1.
Type Locality and Type Material: see *Vrania wagneri* (Kuščer, 1928) in section devoted to taxa of the genus group.

Diagnosis

A species of *Hauffenia* having shell very small, conical-valvatiform or valvatiform, with spire from moderately to well raised; operculum with small peg; penis with one wide lateral lobe.

Material Examined and Description

See *Vrania wagneri* (Kuščer, 1928) in section devoted to taxa of the genus group.

Distribution

Mirna valley, eastern Slovenia.

Taxonomy

The small opercular peg suggests relationships with *Hauffenia media* Bole, 1961. The variability of shell shape suggests that the two taxa may be synonyms. We prefer to maintain them as distinct species, pending further anatomical study of *H. media*.

Hauffenia wienerwaldensis Haase, 1992

Hauffenia wienerwaldensis Haase, 1992: 208–213, figs. 1–11, table 1.
Type Locality: "Upper well in Klamm 106", Wienerwald, Niederösterreich, Austria.
Type Material: holotype (NHMW 85940) and paratypes (NHMW 85941–85946) at the Naturhistorisches Museum Wien, Vienna, Austria; other paratypes are in the Reischütz collection (Baden, Austria) (Haase, 1992).

Diagnosis

A species of *Hauffenia* having shell very small, valvatiform, with spire from almost flat to slightly raised; operculum with very reduced peg; penis without lobes.

Material Examined

—Upper well in Klamm 106, Wienerwald, Niederösterreich, Austria, M. Haase leg. 17.7.1989 (13 shells).

Description

Shell very small, valvatiform, thin, waxen, transparent when fresh; surface of protoconch malleated; spire from almost flat to slightly raised, consisting of 3–3.25 rather rapidly growing convex whorls; last whorl large, dilated, slightly descending near aperture; umbilicus wide; aperture prosocline, oval; peristome complete, thin, slightly reflected only at columellar margin, sometimes detached from last whorl (Fig. 236; Haase, 1992: 208, figs. 1, 2; Boeters, 1998: 29, figs. H9, 10). Dimensions: height = 0.67–1.00 mm; diameter = 1.15–1.69 mm (Haase, 1992: table 1).

Operculum thin, orange, paucispiral, slightly thickened at centre of inner face to give rise to very reduced peg (Haase, 1992: 208, fig. 3A–D).

Body unpigmented (a few black spots on visceral sac); eye spots absent (Haase, 1992: 208, fig. 4).

Male genitalia with penis rather short, large, flat, slightly tapering near apex, ending in a slightly blunt tip and without penial lobes; penial duct zig-zagging through central portion of penis to open near penis tip; no data available about existence of globular mass of refringent cells inside penis apex to right of penial duct; terminal part of penial duct (immediately before opening) with well-developed stylet, which according to original description "stands somewhat behind the tip of penis perpendicular to its axis and slightly inclined to the right" (Haase, 1992: 210, figs. 9–11; Boeters, 1998: 29, fig. H11).

Female genitalia with proximal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle very small, sessile or with very short duct arising from oviduct level with end of loop; bursa copulatrix reduced, same size as seminal receptacle, slightly dilated at apex, arising very close to where oviduct enters albumen gland portion of pallial oviduct; seminal groove running along ventral side of capsule gland (Haase, 1992: 209–210, fig. 8; Boeters, 1998: 29, fig. H12).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with long robust central denticle and 5 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–12 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 19–21 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 15–17 very small denticles (Haase, 1992: 208, fig. 6A, B).

Stomach without posterior caecum; intestine with well-developed, S-like bend on pallial wall (Haase, 1992: 208–209, fig. 7). Haase (1992: 208) reports an "anterior digestive gland lobe" with a separate opening into the stomach.

Osphradium kidney-shaped; ctenidium consisting of 9–10 lamellae; Haase (1992: 208) reports the presence of a hypobranchial gland (Haase, 1992: 208, fig. 5).

Nervous system with long pleuro-supraoesophageal and short pleuro-suboesophageal connectives (Haase, 1992: 209).

Distribution

Niederösterreich, Austria.

Taxonomy

The published data clearly confirms that the present species belongs to *Hauffenia*. As for the hypobranchial gland and the anterior digestive gland-lobe (the latter found by Haase, 1992, in only 25% of dissected specimens), two structures never described before in the group (and which must be more carefully investigated), their meaning for taxonomy appears presently irrelevant.

DESCRIPTIONS OF SOME TAXA MISIDENTIFIED AS *HAUFFENIA* SPECIES

Fissuria raehlei (Schütt, 1980)

Horatia (*Hauffenia*) *raehlei* Schütt, 1980: 140.
Type Locality: "Insel Kephallinia, Schlucht bei Poros, Genist des Baches", Greece.
Type Material: holotype (SMF 263529) at the Senckenberg-Museum, Frankfurt am Main, Germany (Schütt, 1980).

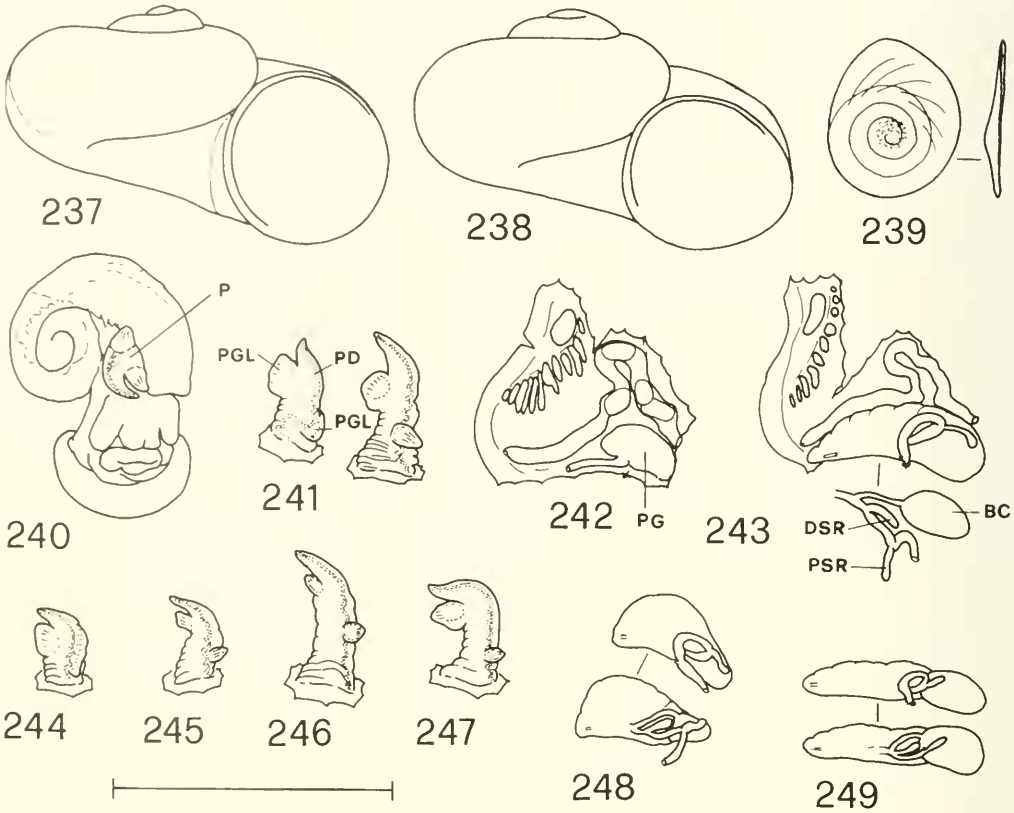
Material Examined

- Well no. G/54, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (1 male, 1 female) (Pesce et al., 1979).
- Well no. G/57, S. Efimia, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (1 male, 1 female) (Pesce et al., 1979).
- Well no. G/58, S. Efimia, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (2 males, 1 shell) (Pesce et al., 1979).
- Well no. G/143, Poros, Cephalonia, Greece, G. L. Pesce, D. Maggi & G. Silverii leg. 2.4.1978 (1 male) (Pesce et al., 1979).
- Well no. G. 174, shore Zante-Lithakial, at the crossroads for Mouzaki, Zante, Greece, G. L. Pesce & G. Silverii leg. 8.4.1979 (1 male, 5 females, 2 shells) (Pesce & Maggi, 1983).
- Well no. G. 194, near Katastarion, Zante, Greece, G. L. Pesce & G. Silverii leg. 9.4.1979 (1 male, 1 female, 2 shells) (Pesce & Maggi, 1983).

Description

Shell very small, valvatiform-planispiral, thin, whitish, transparent when fresh; surface of protoconch malleated; spire slightly raised, consisting of 2.75–3.25 rather rapidly growing, convex whorls; last whorl large, dilated, descending near aperture; umbilicus very wide; aperture prosocline, roundish-ovoid; peristome complete, slightly reflected only at columellar margin (Figs. 237–238; Schütt, 1980: 140, pl. 10a, fig. 42). Dimensions: height = 0.54–1.07 mm; diameter = 1.11–1.52 mm.

Operculum thin, yellowish, paucispiral,



FIGS. 237–249. Shell, operculum and anatomical details of *Fissuria raehlei* (Schütt, 1980) from well no. G/58. S. Efimia, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (Figs. 237, 239, 241–242, well no. G/174, shore Zante-Lithakial, at the crossroads for Mouzaki, Zante, Greece, G. L. Pesce & G. Silverii leg. 8.4.1979 (Figs. 238, 247, 248), well no. G/54, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (Figs. 240, 243, 244), well no. G/57, S. Efimia, Cephalonia, Greece, G. L. Pesce, D. Maggi & M. Miranda leg. 7.5.1977 (Figs. 245, 249) and well no. G/194, near Katastarion, Zante, Greece, G. L. Pesce & G. Silverii leg. 9.4.1979 (Fig. 246). Figs. 237–238: shells; Fig. 239: outer face (left) and profile (centre) of operculum; Fig. 240: body of a male with pallial cavity open to show head and penis; Figs. 241, 244–247: dorsal side of penis of six males; Fig. 242: prostate gland, intestine and pallial organs of a male; Fig. 243: renal and pallial oviduct, intestine and pallial organs of a female; Figs. 248, 249: renal and pallial oviduct of two females. Scale bar = 1 mm.

slightly thickened at centre of inner face but without peg (Fig. 239).

Body unpigmented; eye spots absent (Fig. 240).

Male genitalia with prostate gland bulging well into pallial cavity; penis rather short or moderately long, flat, with apex pointed, and two, well-raised lobes; lobes of variable size and containing mass of glandular tissue: one on left side about 2/3 of penis length; another on dorsal-right side about 1/3 of penis length; penial duct zig-zagging through right portion of penis to open at penis tip (Figs. 241, 242, 244–247).

Female genitalia with two seminal receptacles and a bursa copulatrix arising from distal renal oviduct; proximal and distal seminal receptacles elongated, more or less equal in size; bursa copulatrix variable in size from medium to very large, roundish to oval, with slender elongated duct entering bursa on anterior side; seminal groove running along ventral side of capsule gland (Figs. 243, 248, 249).

Radula with central tooth trapezoidal with long lateral wings and basal tongue; two basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 10–11 denticles, central one longer, larger;

first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 28–32 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of about 22 very small denticles (Figs. 172, 173).

Stomach without posterior caecum; intestine with rather developed, S-like bend on pallial wall (Figs. 242, 243).

Osphradium variable in size, elongated, oval or kidney-shaped; ctenidium consisting of 9–23 lamellae (Figs. 242, 243).

Nervous system unknown.

Taxonomy

The study of many specimens from Cephalonia Island (some collected close to the type locality) and Zante Island revealed that the female genitalia has medium to large bursa copulatrix and two rather long seminal receptacles (proximal and distal) and that the male genitalia have a penis with two glandular lobes. These characters agree with those described for *Fissuria boui* and consequently support inclusion of *Horatia* (*Hauffenia*) *raehlei* in the same genus.

Islamia minuta (Draparnaud, 1805)

Valvata minuta Draparnaud, 1805: 42, pl. 1, figs. 36–38.

Type Locality: no locality is indicated by Draparnaud (1805) or is given in the labels accompanying the type material in the Draparnaud collection at Naturhistorisches Museum Wien (K. Edlinger, pers. com.). It must therefore be assumed that the type locality is "France" from the title of Draparnaud's volume ("Histoire naturelle des mollusques terrestres et fluviatiles de la France"). If the designation of a neotype is ruled by the ICZN, the type locality will become Source de l'Ain, Nozeroy, Jura.

Type Material: original type material consists of the unidentifiable lectotype (a shell) in the Draparnaud collection, Naturhistorisches Museum Wien (Austria) (Binder, 1966). Bernasconi (1975) selected a neotype ["nouveau typoide"] for *Valvata minuta*, but this designation is invalid (see below). In order to preserve this name in the current sense, we are applying to the ICNZ to set aside the type status of the lectotype and to designate the shell shown in Fig. 250 as neotype. The proposed neotype is in the Naturhistorisches Museum Wien (catalogue no. 100485).

Material Examined

- Source de l'Ain, Nozeroy, Jura, M. Bodon leg. 21.7.1985 (3 males, 1 female, many shells).
- Source de l'Epinglier, near Poncin, Ain, M. Bodon leg. 26.8.1989 (1 male, 1 female, 39 shells).
- Source du Dessoubre, Consolation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985 (1 male, 4 females, 48 shells).
- Springs at Consolation-Maisonnettes, Doubs, M. Bodon & G. Manganelli leg. 13.6.1996 (6 males, 14 females, many shells).
- Springs along the stream in the Parc du Seminaire, N.D. de Consolation, Consolation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985 (6 males, 7 females, 27 shells).
- Source de l'Aiguille, Vallon Pont d'Arc, Ardèche, M. Bodon leg. 25.6.1989 (5 males, 3 females, many shells). This population, assigned by Bernasconi (1988) to *I. globulina*, is here reported as *Islamia* cf. *minuta* because anatomically is similar to *I. minuta*, but the shell spire is more conical, like *I. globulina*.

Description

Shell very small, almost planispiral, thin, whitish, waxen, transparent when fresh; surface of protoconch malleated; spire almost flat, consisting of 2.75–3.25 rather rapidly growing, convex whorls: last whorl large, dilated, descending slightly near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, thin, slightly thickened, slightly reflected only at columellar margin (Figs. 209, 250–251; Draparnaud, 1805: 42, pl. 1 figs. 36–38; Locard, 1889: 331–333; 1893: 128; Germain, 1931: 674–675; Binder, 1966: 371–374, figs. 1, 2; Bernasconi, 1975: 308–309, figs. 7a, b, 8a; 1977: 30, figs. 2a, 3a; Boeters, 1998: 28, figs. H1, 2). Dimensions: height = 0.67–1.56 mm; diameter = 1.09–2.11 mm (height = 0.7–1.5 mm; diameter = 1.0–2.2 mm according to Bernasconi, 1975, 1977).

Operculum thin, yellow orange, paucispiral,

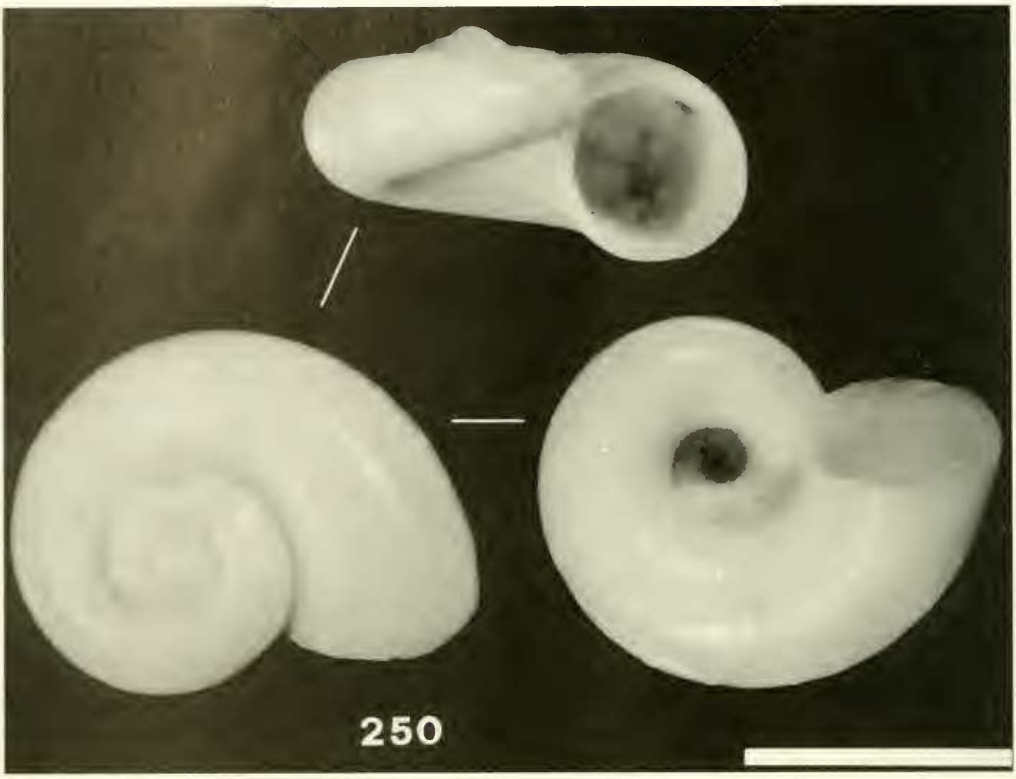


FIG. 250. Proposed neotype of *Islamia minuta* (Draparnaud, 1805) from the Source de l'Ain, Nozeroy, Jura, M. Bodon leg. 21.7.1985. Naturhistorisches Museum Wien (catalogue no. 100485). Scale bar = 1 mm.

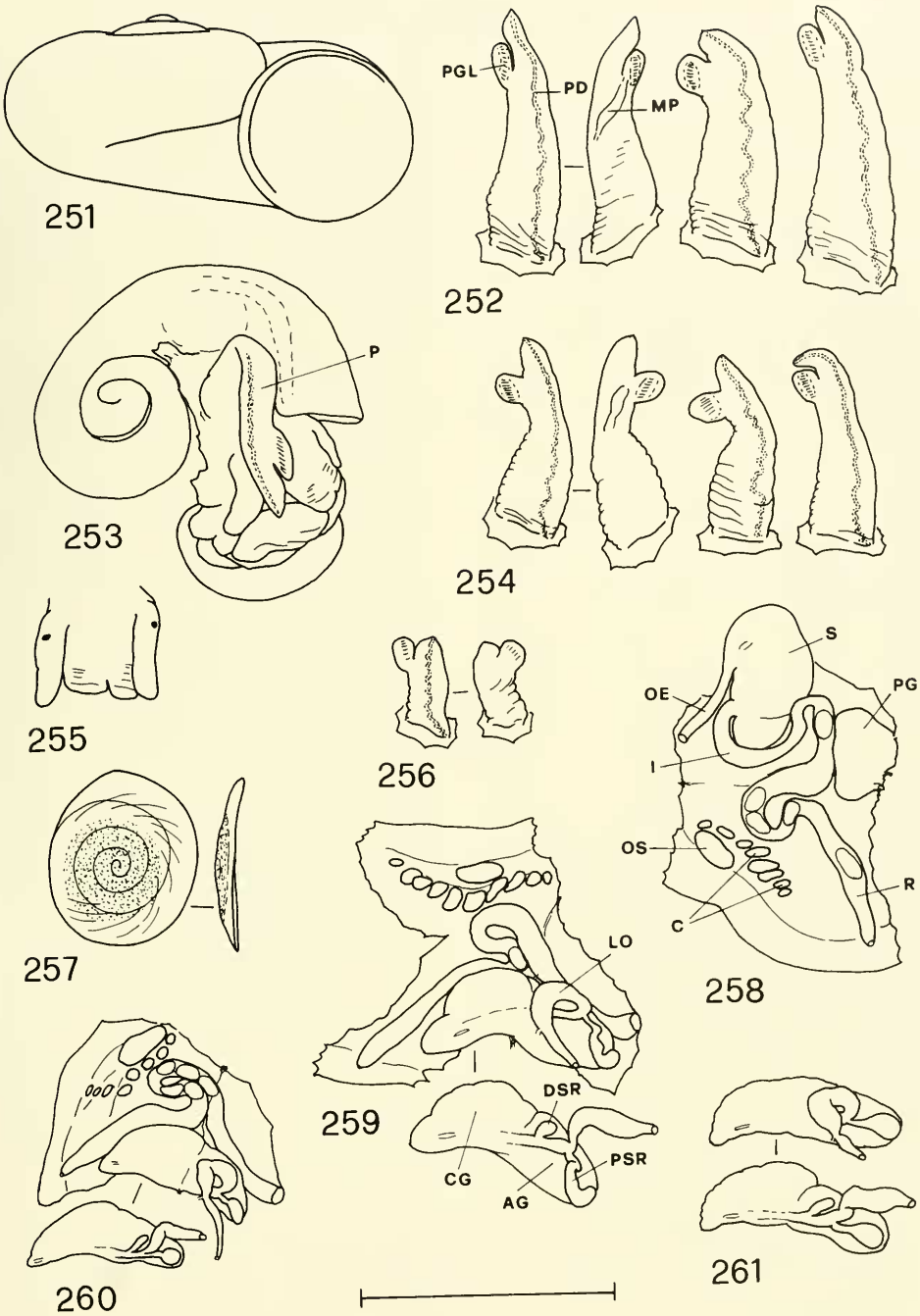
a little thicker at centre but without outgrowth on inner face (Fig. 257; Bernasconi, 1975: 307, fig. 6b, c).

Body unpigmented (sometimes traces of pigment in wall of visceral sac); eye spots present or absent (Figs. 253, 255; Boeters, 1979: 60; Bernasconi, 1975: 304, fig. 1b).

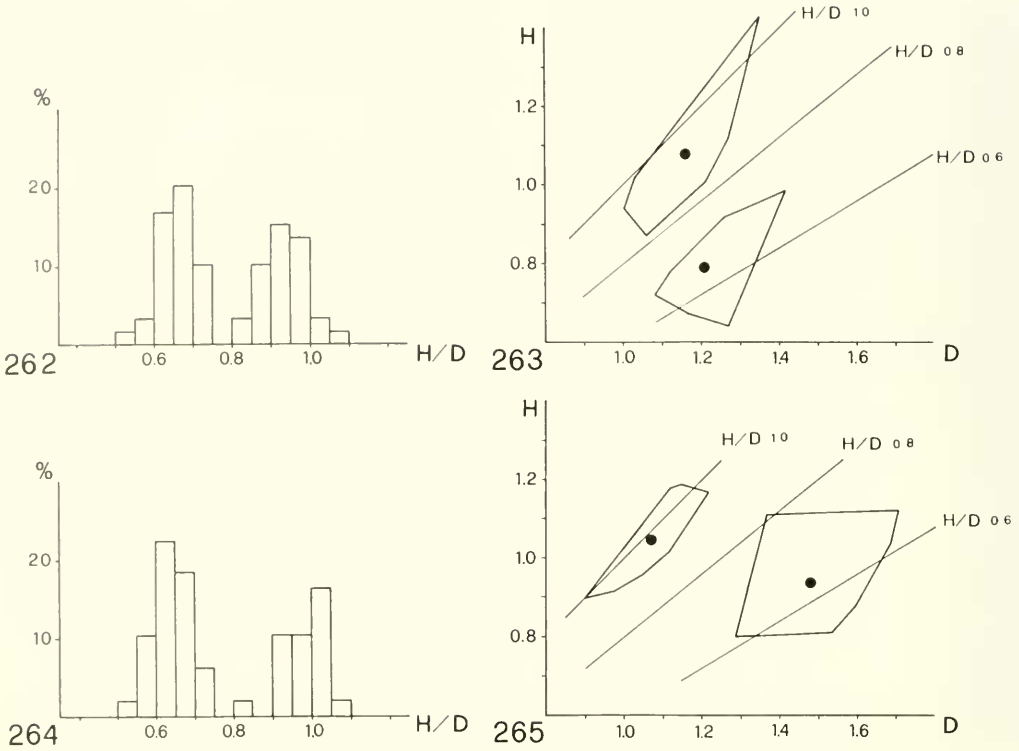
Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather elongated, flat, with sides corrugated near base, not or slightly tapering near apex, which branches in two; right branch corresponding to tip of penis proper, variably elongated, cylindrical or conical, pointed; left branch being a lobe, variable in shape and size, but always shorter than penis tip and with inside refringent mass of glandular cells; rather straight muscular pleat on ventral side about 2/3 of penis length, running obliquely from right side to base of penial lobe and not protruding on left side; penial duct zig-zagging through right or central portion of penis to open at penis tip (Figs. 252, 254, 256; Bernasconi, 1975: 305–306, fig. 4b, c; Boeters, 1998: 28, fig. H4).

Female genitalia with only two seminal receptacles arising from distal renal oviduct, usually not very close to one another; that arising at end of loop (in position corresponding to that of proximal) well developed, always larger and longer than other, with short but evident stalk, wider at apex; that arising close to where oviduct enters albumen gland (in position more or less corresponding to that of distal) very small, usually without evident stalk, in some specimens with refringent mass of oriented spermatozoa; no trace of bursa copulatrix; seminal groove running along ventral side of capsule gland (Figs. 259–261; Bernasconi, 1975: 306, fig. 5b; Boeters, 1998: 28, fig. H5).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with larger central denticle and five smaller denticles on both sides in decreasing order of size; 2–3 basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 11–13 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 20–26



FIGS. 251–261. Shell, operculum and anatomical details of *Islamia minuta* (Draparnaud, 1805) from the Source de l'Ain, Nozeroy, Jura, M. Bodon leg. 21.7.1985 (Figs. 251–253, 255, 257, 259), from the springs along the stream in the Parc du Seminaire, N.D. de Consolation, Consolation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985 (Figs. 254, 261), and from the Source de l'Epinglier, near Poncin, Ain, M. Bodon leg. 26.8.1989 (Figs. 256, 260). Fig. 251: shell; Figs. 252, 254, 256: dorsal and ventral side (the second picture of each series) of penis of seven males; Fig. 253: body of a male with pallial cavity open to show head and penis; Fig. 255: head of another specimen with eye spots; Fig. 257: outer face (left) and profile (right) of operculum; Fig. 258: prostate gland, stomach, intestine and pallial organs of a male; Figs. 259, 260: renal and pallial oviduct, intestine and pallial organs of two females; Fig. 261: renal and pallial oviduct of a female. Scale bar = 1 mm.



FIGS. 262–265. Biometric analysis of the shells of some populations of the French *Islamia*. Figs. 262, 263: *I. minuta* (Draparnaud, 1805) and *I. globulina* (Paladilhe, 1866) from the Source de l'Epinglier, near Poncin, Ain, M. Bodon leg. 26.8.1989; Figs. 264, 265: *I. minuta* and *I. spirata* (Bernasconi, 1985) from the springs along the stream in the Parc du Seminaire, N.D. de Consolation, Consolation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985. H: shell height; D: shell diameter; dimensions in mm.

small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 14–18 very small denticles (Bernasconi, 1975: 304–305, fig. 2b, c).

Stomach without posterior caecum; intestine with well-developed, S-like bend on pallial wall (Figs. 258–260; Bernasconi, 1975: 306, fig. 3b; Boeters, 1998: 28, fig. H3).

Osphradium oval; ctenidium consisting of 8–14 lamellae (Figs. 258–260; Bernasconi, 1975: 305, fig. 3b).

Nervous system unknown.

Distribution

The distribution of *Islamia* in France includes a large part of the Rhone basin to the east, the Languedoc and the Garonne, Dordogne basins and probably the Gascogne (Fig. 185) to the southwest. The distribution indicated by Bouchet (1990: Fig. 7) for "*Hauffenia*" *minuta* and by Ripert (1998: fig. 10) for "*Neohoratia*" *globulina* includes eastern Provence and the Côte d'Azur, southeastern areas in which *Islamia* has never been documented (anatomical study of valvatiform hydrobiids from the Départements of Vaucluse, Var and Alpes Maritimes, identified them as *Fissuria boui* Boeters, 1982).

Populations surely attributed to *I. minuta* have only been found in the Jura mountains, the upper Rhone basin, the French départments of Doubs, Jura and Ain and the Swiss cantons of Neuchâtel and Bern (Bernasconi, 1975, 1977).

Taxonomy

Our study shows that the relative position of the two seminal receptacles and the point where they arise from the renal oviduct are quite constant in all the populations examined

of *Islamia minuta, I. globulina* (Paladilhe, 1866), *I. spirata* (Bernasconi, 1975) and *I. consolationis* (Bernasconi, 1985) (for the last three, see Descriptions below). It is important that the proximal seminal receptacle is always larger and longer than the distal one (see Description of *Islamia*). This contrasts with what Bernasconi (1975, 1977, 1984, 1985) claimed, that is, distal sac-like structure (arising from renal oviduct just before it enters pallial oviduct) larger than proximal (arising close to end of loop). The fact that at least part of the material studied by Bernasconi comes from the same localities as the material studied by us (Source de l'Ain, Nozeroy for *I. minuta;* Vidourle, résurgence, Sauve for *I. globulina*) indicates that our material cannot belong to a taxon different from Bernasconi's and suggests that he misinterpreted the female genital structure. This may have been because in wrongly interpreting the larger sac-like structure as a bursa copulatrix, Bernasconi illustrated it arising where the bursa copulatrix normally arises in the hydrobiids, that is, from the renal oviduct immediately before the oviduct enters the pallial oviduct. This misinterpretation is indirectly confirmed by the fact that the position of the smaller sac-like structure, interpreted by Bernasconi as a seminal receptacle, is also imprecisely figured by him. In Bernasconi's figures, it does not have a constant position and sometimes arises proximally from the renal oviduct at the end of the loop and sometimes about halfway along the loop (see Bernasconi, 1975, fig. 5; 1977, fig. 1e; 1984, fig. 1e; 1985, fig. 1d).

Our data on the structure of the female genitalia and the penis (presence of glandular lobe on left side of penis; absence of mass of refringent cells inside penis apex to right of penial duct; absence of stylet at tip of penis) is enough to conclude that these French species do not belong to *Hauffenia,* as Haase (1993: 106) suggested. The misinterpreted French "*Hauffenia*" must be assigned to *Islamia.* In fact, they only differ from the type species of *Islamia* from the Balkans (to which species from Italy, Asia Minor and Middle East are more or less related; cf., Radoman, 1973a, 1983; Giusti & Pezzoli, 1980; Giusti et al., 1981; Schütt, 1991; Bodon et al. 1995a) in some minor anatomical features: for example, seminal receptacles sometimes more distant from one another and relatively undeveloped muscular pleat on ventral side of penis which does not protude on left side.

It is particularly difficult to clarify the identity of *Valvata minuta* and the status of the forms/subspecies into which it has been subdivided. *Valvata minuta* is cited by many classic authors from various localities (Férussac, 1807: 128; Bouchard-Chantereaux, 1838: 87; Gassies, 1849: 183; 1859: 60; Dupuy, 1851: 585–586; Moquin-Tandon, 1856: 434). Paladilhe (1866: 25, 27) claimed that Gassies and the others misinterpreted it as "une charmante Valvée microscopique de forme globuleuse", which he described as a distinct species: *V. globulina.* Locard (1895: 20, 46–47) traced the type material of *V. minuta.* This consists of two shells in the Draparnaud collection in the Naturhistorisches Museum Wien, Austria, and one in the M. Bischof von Hohenwarth collection. Many years later, Binder (1966: 371–372) studied the two syntypes in the Naturhistorisches Museum Wien. One is a hydrobiid species (and is selected as the "type"), the other is a fragment of the apex of a shell of *Valvata piscinalis* (Müller, 1774).

Bernasconi (1975) published a first redescription of *V. minuta* based on the study of some Swiss and French populations, but his paper contains many controversial aspects which have made a puzzle of the case. First of all, although he was aware of the existence of a lectotype, Bernasconi selected a neotype ["nouveau typoide"] for *V. minuta,* in contravention of ICZN (1999: Art. 75) and consequently invalid. Moreover, his neotype does not belong to the nominotypical form/subspecies *minuta* but to the different form/subspecies *globulina.* The type locality indicated for the form/subspecies *globulina* (Vidourle, résurgence (Sauve)), and not that of the form/subspecies *minuta* (Areuse, résurgence (St. Sulpice)), is reported as type locality of the species. Both these restricted type localities are outside the range reported by the authors of the taxa. In fact, that of the form/subspecies *minuta* is in the Swiss canton of Neuchâtel (under the king of Prussia until 1815) and not in France; that of form/subspecies *globulina* in the Rhone basin, and not in the Garonne basin. As a consequence, his neotype designation and his type locality restriction are invalid.

Study of the lectotype (Draparnaud collection no. 1820 xxvi/21; Naturhistorisches Museum Wien, Austria; Binder, 1966: fig. 1) does not enable certain identification of the species. It has a shell shape similar to the specimens of *I. minuta* from the Jura, but the shell

TABLE 8. Shell parameters of the *Islamia* species coexisting in the Source de l'Epinglier at Poncin, Ain, and the springs in the Parc du Seminaire at Consolation-Maisonnettes, Doubs. Acronyms: H shell height, D shell diameter.

Locality	Taxa	
Source de l'Epinglier, Poncin (Ain)	*Islamia minuta*	*Islamia globulina*
mean ratio H/D ± σ	0.65 ± 0.05	0.93 ± 0.06
(range)	(0.51–0.73)	(0.82–1.06)
number of shells	31	28
Springs in the Parc du Seminaire, Consolation-Maisonnettes (Doubs)	*Islamia minuta*	*Islamia spirata*
mean ratio H/D ± σ	0.62 ± 0.06	0.98 ± 0.04
(range)	(0.53–0.81)	(0.91–1.06)
number of shells	30	19

height is less. On the basis of shell size (height: 0.60 mm; diameter: 1.34 mm), it is more similar to *Valvata exilis* Paladilhe, 1867, from the Département de l'Hérault (see "Description of a new valvatiform genus from France" for redescription of *V. exilis*), differing in the fact that the last whorl is not dilated near the aperture. No locality is indicated by Draparnaud (1805), nor is it given in the labels accompanying the type material in the Draparnaud collection. If Draparnaud, who lived in Montpellier, collected this material near his town, then his *V. minuta* cannot be the species that is currently considered to be *V. minuta,* which lives much further north, but it may be *V. exilis.* In this situation, we think that it is better to apply to ICZN to set aside the Binder's (1966) type designation and to designate a neotype for this species so that the current understanding of this nominal taxon is preserved.

The proposed neotype (Fig. 250) was collected in the Source de l'Ain, Nozeroy, Jura. This proposed neotype (a shell) was chosen from a population for which the anatomy is already known (Bernasconi, 1975). This population lives in a major spring of the French Jura. No other similar *Islamia* species lives in the same spring. The neotype is deposited in the Naturhistorisches Museum Wien (catalogue no. 100485).

Bernasconi (1984, 1985, 1988) regarded *I. minuta* as having four subspecies. All of them, apart from *I. consolationis,* which is characterized by a larger shell, are identified by different values of the ratio of shell height and diameter (H/D) (*I. minuta:* 0.56 ± 0.07–0.66 ± 0.09; *I. globulina:* 0.76 ± 0.09–0.91 ± 0.06; *I. spirata:* 1.00 ± 0.06–1.07 ± 0.08; Bernasconi, 1975, 1985). In cases of coexistence of more forms/subspecies, shell material clearly revealed that the populations are not homogeneous and that the frequencies of H/D values are distributed on a bimodal curve. For example, the population from Source de l'Epinglier, Ain, consists of two quite distinct shell morphs (Table 8; Figs. 262, 263). Binder (1966) studied the shells and claimed that the depressed shells, traditionally assigned to *V. minuta,* and the shells with raised spire, traditionally assigned to *V. globulina,* were linked by a series of intermediate shells, and were the extremes of a continuum. He concluded that *V. minuta* and *V. globulina* were not distinct species ("Cette distinction ne se justifie probablement pas . . ."). The evidence of two distinct coexisting morphs is undeniable in this population. Unfortunately, there is too little anatomical data, only one female and one male (Fig. 256) examined, to confirm their status as distinct taxa on an anatomical basis. If we are to accept the H/D criteria of Bernasconi (1975, 1985), these two morphs can be assigned to *I. minuta* and to *I. globulina.*

The same happens near Consolation-Maisonnettes, Doubs, where three distinct shell morphs also coexist (Table 8; Figs. 264, 265). Again, according to the dimensions and the H/D values of Bernasconi (1975, 1985), the three morphs can be assigned to *I. minuta,* to *I. spirata* and to *I. consolationis.* Anatomical study revealed that the specimens attributed to *I. minuta* and *I. consolationis* have a penial lobe shorter than the penial apex, and those assigned to *I. spirata* a penial lobe longer than the penial apex, while only *I. minuta* has eye spots (Figs. 254, 276–277, 282, 284).

Other specimens such as those collected in the Source de l'Aiguille, Vallon Pont d'Arc,

Ardèche, and assigned by Bernasconi (1988) to *I. globulina* are characterized by H/D values (mean H/D: = 0.76 ± 0.05), which lie almost between those of *I. globulina* and *I. minuta* whereas the male genitalia, are identical to those of *I. minuta* (penial lobe shorter than penis apex).

Islamia spirata is readily distinguishable by shell parameters only in the case of the type population. When other populations are considered the distinction becomes problematical. As well, the absence of eyes in the type population of *I. spirata* is of no help for distinguishing it from *I. globulina.* In fact, other populations assignable to *I. minuta* or *I. globulina* contained specimens with eyes coexisting with specimens without eyes, suggesting that this character is occasionally variable.

The above facts are evidence of a very complex situation and possibly of equivocal shell and anatomical characters. However, since almost all these taxa (except *I. globulina* and *I. spirata*) live together in some places and are distinguishable by morphometric and anatomical characters, there must be at least three distinct species. More populations must obviously be studied (especially from the type localities of all the taxa described in the past) in order to gather more biometric and anatomical data for a better understanding of the taxonomic setting of the group. We nevertheless feel justified in rejecting the current interpretation of all French *Islamia* as subspecies of *I. minuta.* We suggest provisional recognition of the four taxa, *I. minuta* (Draparnaud, 1805), *I. globulina* (Paladilhe, 1866), *I. spirata* (Bernasconi, 1975), and *I. consolationis* (Bernasconi, 1985) as distinct species (see key in Table 9, Fig. 266).

The shells of the different species of *Islamia* described to date (Radoman, 1973a, 1983; Giusti & Pezzoli, 1980; Giusti et al., 1981; Schütt, 1991; Bodon et al., 1995a) vary little in shape (mostly valvatiform with the spire raised to different degrees) and size. These two characters are not sufficiently diagnostic to determine the status of allopatric taxa. This obviously compels us to rely on anatomy, which also offers little in the way of diagnostic characters. Apart from the fact that French *Islamia* colonize an area geographically separate from the other areas inhabited by this genus (Spain, Italy, Corsica, Elba, Sicily, Balkans, Turkey, and Israel), two characters seem to confirm their distinctiveness. These characters, if constant, would be sufficient to support the existence of a distinct branch in the radiation of *Islamia.* In fact, the French *Islamia* are distinguished from all the eastern species, from the Balkans to Turkey and Israel (Radoman, 1973a, 1983; Giusti et al., 1981; Schütt, 1991), by seminal receptacles, on the average, more distant from one another and a relatively undeveloped muscular pleat on ventral side of penis, not protruding on left side as in typical *Islamia.* The same differences distinguish the French *Islamia* from the Italian *I. pusilla* (Piersanti, 1952) (Giusti et al., 1981), while a markedly reduced penial lobe distinguishes two other recently described *Islamia* species

TABLE 9. Provisional analytical key for the identification of French *Islamia* species. For characters used, see Fig. 266.

1a – Penial lobe shorter than penis apex	2
1b – Penial lobe longer than penis apex	3
2a – Mean D < 2 mm; mean H/D = 0.56–0.66	*I. minuta*
2b – Mean D > 2 mm; mean H/D = 0.80–0.90	*I. consolationis*
3a – Mean H/D = 0.76–0.93	*I. globulina*
3b – Mean H/D = 0.98–1.07	*I. spirata*

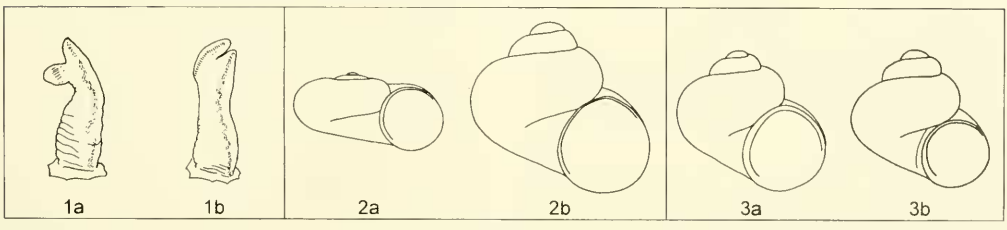


FIG. 266. Characters used in the analytical key for the identification of the French *Islamia* species (Table 9).

from different Italian islands: *I. cianensis* Bodon, Manganelli, Sparacio & Giusti, 1995 (penis with muscular pleat), and *I. gaiteri* Bodon, Manganelli, Sparacio & Giusti, 1995 (penis without muscular pleat; Bodon et al., 1995a). Finally, other undescribed or little known Italian (see Giusti et al., 1981), Corsican and Spanish taxa differ in other anatomical characters and/or the frequent absence of a muscular pleat on the ventral side of penis (for the Spanish species, see above).

Islamia globulina (Paladilhe, 1866)

?*Valvata moquiniana* Dupuy, 1851: 586–587, pl. 28, fig. 15.
Type Locality: ". . . alluvions du Lot, près de Mende . . .", Dep. Lozère, France.
Type Material: Dupuy (1851) did not give any information about the type material.
Valvata globulina Paladilhe, 1866: 170 [p. 27 in reprint].
Type Locality: ". . . paraît spéciale au bassin de la Garonne, notamment dans les départements du Gers et de Lot-et-Garonne.", France.
Type Material: Paladilhe (1866) did not give any information about the type material; Binder (1966) stated that the type does not exist.
?*Valvata bourguignati* Letourneux, 1869: 197–199.
Type Locality: ". . . fontaine, près du Moulin-Gachet (commune de Pissotte)", Dep. Vendée, France.
Type Material: Letourneux (1869) did not give any information about the type material.
?*Valvata turgidula* Locard, 1889: 333–334.
Type Locality: ". . . lac de la Négresse, près de Bayonne, dans les Basses-Pyrénées . . .", France.
Type Material: according to Locard (1889) type material is in the Bourguignat collection, Geneve, Switzerland.
?*Valvata micrometrica* Locard, 1889: 336–337.
Type Locality: ". . . fontaine du Camarde, près de Valence dans le Gers", France.
Type Material: Locard (1889) did not give any information about the type material.

Material Examined

– Source de l'Epinglier, near Poncin, Ain, M. Bodon leg. 26.8.1989 (34 shells).
– Vidourle, résurgence, Sauve, Gard, 1.1976, *ex* R. Bernasconi collection (2 males, 2 females); M. Bodon leg. 2.12.1984 (3 shells).
– Source de la Nizon, Lirac, Gard, M. Bodon, H. Girardi & B. Bomba leg. 29.12.1998 (3 males, 1 female, many specimens, many shells).
– Wells 13/PT/2, propriété Michon, Chateaurenard, Bouches du Rhône, C. Bou leg. 4.1977, collection H. Girardi (1 male).
– Résurgence du Moulis at Moulis, St. Girons, Ariège, M. Bodon leg. 13.9.1985 (1 male, 2 females, 1 shell).
– Rivière souterraine de Labouiche, Foix, Ariège, M. Bodon leg. 13.9.1985 (1 male, 2 females, many shells).
– Ruisseau souterrain d'Amiel, Penne, Tarn, C. Bou leg. 12.1991, ex H. Girardi collection (3 males, 1 female).
– Ruisseau souterrain de Cabeau, Penne, Tarn, C. Bou leg. 12.1976, H. Girardi collection (1 male, 1 female).
– Source de la Mandre, Soreze, Tarn, C. Bou leg. 10.1991, H. Girardi collection (1 male, 6 shells).
– Water-bearing stratum of the intake A.E.P. of Lescure, Tarn, C. Bou leg. 12.1991, *ex* H. Girardi collection (5 males, 2 females).
– Fontaine des Canelles, Lalinde, Dordogne, M. Bodon leg. 27.6.1989 (1 female). This population is reported as *Islamia* cf. *globulina,* because there were no male specimens for anatomical study.

Description

Shell very small, valvatiform, thin, whitish, waxen, transparent when fresh; surface of protoconch malleated; spire rather raised, consisting of 2.5–3.25 rather rapidly growing, convex whorls; last whorl large, dilated, descending slightly near aperture; umbilicus small; aperture prosocline, roundish; peristome complete, thin, slightly thickened, slightly reflected only at columellar margin (Figs. 210, 267; Gassies, 1849: 183, pl. 2, fig. 7, as *V. minuta;* Moquin-Tandon, 1855: 543, pl. 41, figs. 26–28, as *V. minuta;* Locard, 1889: 334–336, 1893: 127–128, fig. 130; Dupuy, 1851: 585, pl. 28, fig. 14, as *V. minuta;* Germain, 1931: 675–676, figs. 742, 743; Binder, 1966: 371–374, figs. 2, 3; Bernasconi, 1975: 308, 310, figs. 7c, 8b; 1977: 30, figs. 2a, 3a; 1984: 205, fig. 7f). Dimensions: height = 0.7–1.8 mm; diameter = 0.9–1.9 mm (height and diameter according to Bernasconi, 1975, 1977).

Operculum thin, pale yellowish or yellow,

paucispiral, a little thicker at centre but without outgrowth on inner face (Fig. 268; Boeters, 1973: 65; Bernasconi, 1975: 307, fig. 6a; 1984: fig. 1b).

Body unpigmented (sometimes traces of pigment in wall of visceral sac); eye spots present or absent (Fig. 269; Boeters, 1973: 65; Bernasconi, 1975: 304, fig. 1a; 1984: fig. 1a).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis variably elongated, flat, with sides corrugated near base, not or slightly tapering near apex, which branches in two: right branch, forming tip of penis proper, short, conical, more or less pointed; left branch constituting lobe, variable in shape and size but always slightly longer than penis tip, with inside refringent mass of glandular cells; rather straight muscular pleat on ventral side about 2/3 of penis length, running obliquely from right side to base of penial lobe, not protruding on left side; penial duct zig-zagging through right or central portion of penis to open at penis tip (Figs. 270, 271; Boeters, 1973: 65; Bernasconi, 1975: 305–306, fig. 4a; 1984: fig. 1a, d).

Female genitalia with only two seminal receptacles arising from distal renal oviduct, usually not very close to one another; that arising at end of loop (in position corresponding to that of proximal) well developed, always larger and longer than other, with short but evident stalk and apical enlargement; that arising close to where oviduct enters albumen gland (in position more or less corresponding to that of distal) very small, usually without evident stalk; no trace of bursa copulatrix; seminal groove running along ventral side of capsule gland (Figs. 272, 273; Boeters, 1973: 65; Bernasconi, 1975: 306, fig. 5a; 1984: fig. 1e).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like, with larger central denticle and 5 smaller denticles on both sides, in decreasing order of size; 2–3 basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 11–13 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 20–26 small denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 14–18 very small denticles (Bernasconi, 1975: 304–305, fig. 2a).

Stomach without posterior caecum; intestine with well developed, U- or S-like bend on pallial wall (Figs. 272, 274; Boeters, 1973: 65; Bernasconi, 1975: 306–307, fig. 3a).

Osphradium variable in size, oval or elongated; ctenidium consisting of 6–11 lamellae (Figs. 272, 274; Boeters, 1973: 65; Bernasconi, 1975: 305, fig. 3a; 1984: fig. 1c).

Nervous system unknown.

Distribution

The distribution of *I. globulina* includes much of France: the Rhone basin to the east, and the Languedoc, the Garonne and Dordogne basins and probably the Gascogne to the southwest (Bernasconi, 1975, 1977; Bertrand, 1998; Ripert, 1998).

Taxonomy

See also discussion of *I. minuta*. All the *Islamia* populations from southern France having shell characters of *I. globulina* can be considered to belong to the same species on the basis of anatomical characters.

Although, it has not been studied topotypical material of all nominal species, having *globulina*-like shell described from southern France (e.g., *Valvata moquiniana* Dupuy, 1851; *V. globulina* Paladilhe, 1866; *V. bourguignati* Letourneux, 1869; *V. turgidula* Locard, 1889; and *V. micrometrica* Locard, 1889), it is very probable that they are synonymous. If this is true, the oldest established name available for this taxon is *V. moquiniana*. Here we have maintained its current name *V. globulina*, awaiting a definitive revision, including the study of material from the Départments of Gers and Lot-et-Garonne, the type locality of the species described by Paladilhe (1866).

Islamia spirata (Bernasconi, 1985)

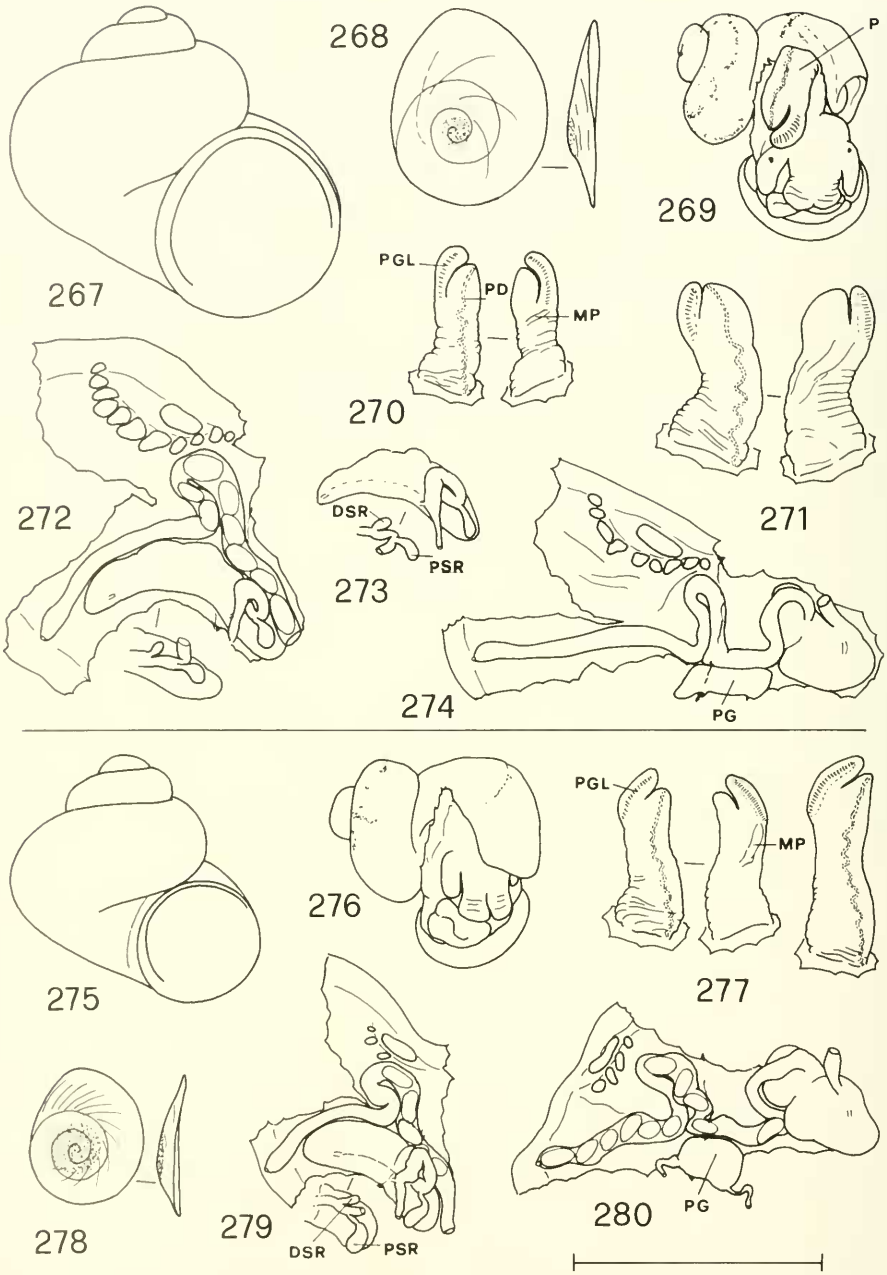
Hauffenia minuta spirata Bernasconi, 1985: 63–64, fig. 1a–e, table 1.

Type Locality: "Bléfond, résurgence (Silley; V. 3)", Dép. Doubs, France.

Type Material: Bernasconi (1975) did not give any information about the type material.

Material Examined

–Springs along the stream in the Parc du Seminaire, N.D. de Consolation, Conso-



FIGS. 267–280. Shell, operculum and anatomical details of *Islamia globulina* (Paladilhe, 1866) from Vidourle, résurgence, Sauve, Gard, France 1.1976, *ex* R. Bernasconi collection (Figs. 267, 268, 271–272, 274) and from the Résurgence du Moulis at Moulis, St. Girons, Ariège, France, M. Bodon leg. 13.9.1985 (Figs. 269, 270, 273) and of *Islamia spirata* (Bernasconi, 1985) from the springs along the stream in the Parc du Seminaire, N.D. de Consolation, Consolation-Maisonnettes, Doubs, France, M. Bodon leg. 21.7.1985 (Figs. 275–280). Figs. 267, 275: shells; Figs. 268, 278: outer face (left) and profile (right) of operculum; Figs. 269: body of a male with pallial cavity open to show head and penis; Figs. 270, 271, 277: dorsal and ventral side (second picture of each series) of penis of four males; Figs. 272, 279: renal and pallial oviduct, intestine and pallial organs of a female; Fig. 273: renal and pallial oviduct of a female; Figs. 274, 280: prostate gland, stomach, intestine and pallial organs of a male; Fig. 276: body of a female with pallial cavity open to show head. Scale bar = 1 mm.

lation-Maisonnettes, Doubs, France, M. Bodon leg. 21.7.1985 (4 males, 7 females, 9 shells).
– Stream near Pont les Moulins, Cusancin valley, Doubs, France, M. Bodon leg. 22.7.1985 (many shells).

Description

Shell very small, valvatiform, thin, whitish, waxen, transparent when fresh; surface of protoconch malleated; spire raised, consisting of 3–3.5 rather rapidly growing, convex whorls; last whorl large, dilated, descending slightly near aperture; umbilicus small; aperture prosocline, roundish; peristome complete, thin, slightly thickened, slightly reflected only at columellar margin (Figs. 211, 275; Bernasconi, 1975: 308, 310, figs. 7d, 8c; 1985: table 1, fig. 2). Dimensions: height = 0.90–1.51 mm; diameter = 0.90–1.44 mm (height = 1.0–1.9 mm; diameter = 1.0–1.8 mm, according to Bernasconi, 1975).

Operculum thin, yellowish, paucispiral, a little thicker at centre but without outgrowth on inner face (Fig. 278; Bernasconi, 1985: 63, fig. 1a).

Body unpigmented (sometimes traces of pigment in wall of visceral sac); eye spots absent (Fig. 276; Bernasconi, 1985: 63).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather elongated, flat, with sides corrugated near base, tapering slightly near apex, which branches into two; right branch, forming tip of penis proper, short, conical, more or less pointed; left branch, constituting lobe, cylindrical, slightly longer than penis tip, with inside refringent mass of glandular cells; rather straight muscular pleat on ventral side about 2/3 of penis length, running obliquely from right side to base of penial lobe, not protruding on left side; penial duct zig-zagging through right or central portion of penis to open at penis tip (Fig. 277; Bernasconi, 1985: 63–64, fig. 1e).

Female genitalia with only two seminal receptacles arising from distal renal oviduct, rather close to one another: that arising at end of loop (in position corresponding to that of proximal) well developed, always larger, longer than other, with short but evident stalk and apical enlargement; that arising close to where oviduct enters albumen gland (in position more or less corresponding to that of distal) very small, usually without evident stalk; no trace of bursa copulatrix; seminal groove running along ventral side of capsule gland (Fig. 279; Bernasconi, 1985: 64, fig. 1d).

Radula details unknown (Bernasconi, 1985: 63).

Stomach without posterior caecum; intestine with well-developed, S-like bend on pallial wall (Figs. 279, 280; Bernasconi, 1985: 64, fig. 1b, c).

Osphradium variable in size, oval or elongated; ctenidium consisting of 3–10 lamellae (Figs. 279, 280; Bernasconi, 1985: 63, fig. 1b).

Nervous system unknown.

Distribution

The distribution of *I. spirata* is limited to a small area in the Jura mountains, upper Rhone basin, in the French Département of Doubs (Bernasconi, 1975, 1985).

Taxonomy

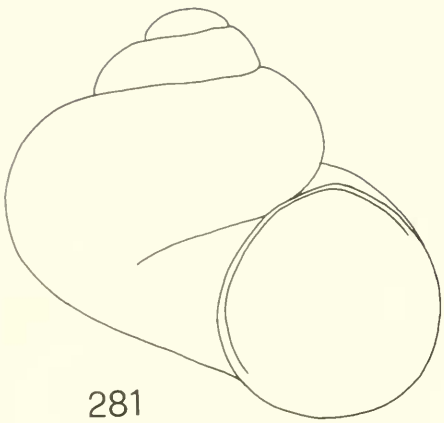
See discussion of *I. minuta.*

***Islamia consolationis* (Bernasconi, 1985)**

Hauffenia minuta consolationis Bernasconi, 1985: 64, figs. 2, 3, table 2.
Type Locality: "Maurepos, . . . bei Consolation-Maisonettes," Doubs, France.
Type Material: holotype at Museum d'Histoire Naturelle de Genève, Geneva, Switzerland; paratypes are in the Bernasconi collection, Münchenbuchsee, Switzerland (Bernasconi, 1985).

Material Examined

– Grotte du Biez-Airoux, Consolation-Maisonnettes, Doubs, M. Bodon & G. Manganelli leg. 13.6.1996 (3 males, 2 females, 10 shells).
– Grotte de Maurepos, Consolation-Maisonnettes, Doubs, M. Bodon & G. Manganelli leg. 13.6.1996 (1 shell).
– Source du Dessoubre, Consolation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985 (many shells), M. Bodon & G. Manganelli leg. 13.6.1996 (2 females, 17 shells).
– Springs at Consolation-Maisonnettes, Doubs, M. Bodon & G. Manganelli leg. 13.6.1996 (many shells).
– Springs along the stream in the Parc du Seminaire, N.D. de Consolation, Conso-



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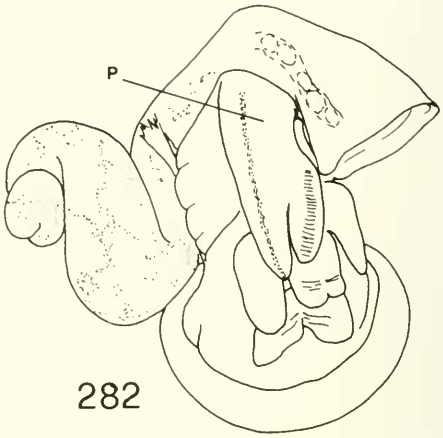

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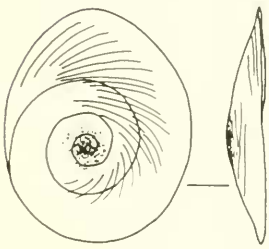

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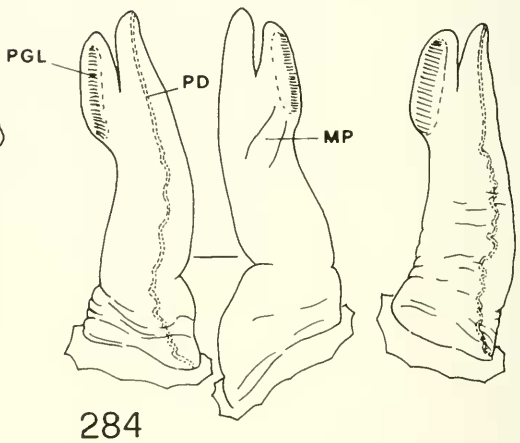

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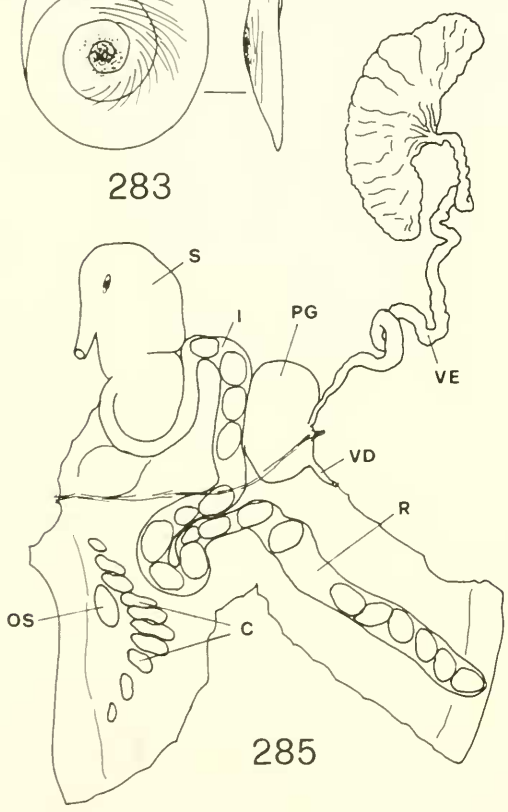

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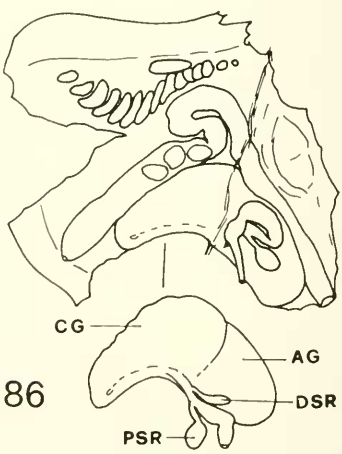

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FIGS. 281–286. Shell, operculum and anatomical details of *Islamia consolationis* (Bernasconi, 1985) from the Grotte du Biez-Airoux, Consolation-Maisonnettes, Doubs, France, M. Bodon & G. Manganelli leg. 13.6.1996. Fig. 281: shell; Fig. 282: body of a male with pallial cavity open to show head and penis; Fig. 283: outer face (left) and profile (right) of operculum; Fig. 284: dorsal and ventral side (second picture) of penis of two males; Fig. 285: testis, vas efferens, prostate gland, stomach, intestine and pallial organs of a male; Fig. 286: renal and pallial oviduct, intestine and pallial organs of a female. Scale bar = 1 mm.

lation-Maisonnettes, Doubs, M. Bodon leg. 21.7.1985 (3 shells).

Description

Shell very small, valvatiform, thin, whitish, waxen, transparent when fresh; surface of protoconch very finely malleated; spire rather raised, consisting of 2.75–3.5 rather rapidly growing convex whorls; last whorl large, dilated, descending slightly near aperture; umbilicus small; aperture prosocline, roundish; peristome complete, thin, slightly thickened, slightly reflected only at columellar margin (Figs. 212, 281; Bernasconi, 1985: table 2, fig. 3). Dimensions: height = 1.80–2.80 mm; diameter = 1.94–2.79 mm (height =1.63 ± 0.53–2.09 ± 0.15 mm; diameter = 2.01 ± 0.36–2.32 ± 0.21 mm according to Bernasconi, 1985).

Operculum thin, yellow orange, paucispiral, a little thicker at centre but without outgrowth on inner face (Fig. 283).

Body unpigmented (traces of pigment in wall of visceral sac); eye spots usually absent (Fig. 282).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather elongated, flat, with sides corrugated near base, not or slightly tapering near apex, which branches in two; right branch, forming tip of penis proper, variably elongated, conical, more or less pointed; left branch constituting lobe, cylindrical, shorter than penis tip, with inside refringent mass of glandular cells; rather straight muscular pleat present on ventral side at about 3/4 the penis length, running obliquely from right side to base of penial lobe, not protruding on left side; penial duct zig-zagging through right or central portion of penis to open at penis tip (Fig. 284).

Female genitalia with only two seminal receptacles arising from distal renal oviduct, rather close to one another: that arising at end of loop (in position corresponding to that of proximal) well developed, always larger, longer than other, with short but evident stalk and apical enlargement; that arising close to where oviduct enters albumen gland (in position more or less corresponding to that of distal) small, without evident stalk; no trace of bursa copulatrix; seminal groove running along ventral side of capsule gland (Fig. 286).

Radula with central tooth trapezoidal, with long lateral wings and basal tongue, its apical margin V-like with long, robust central denticle and 5 smaller denticles on both sides in decreasing order of size; 1–2 basal cusps where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 15–17 long denticles anteriorly; second marginal teeth scraper-shaped, with long, slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of about 15 small denticles (Figs. 174–176).

Stomach without posterior caecum; intestine with well-developed, S-like bend on pallial wall (Figs. 285, 286).

Osphradium variable in size, oval or elongated; ctenidium consisting of 10–15 lamellae (Figs. 285, 286).

Nervous system unknown.

Distribution

The distribution of *I. consolationis* is limited to a small area in the Jura mountains, upper Rhone basin, in the French Département of Doubs (Bernasconi, 1985).

Taxonomy

See discussion of *I. minuta*.

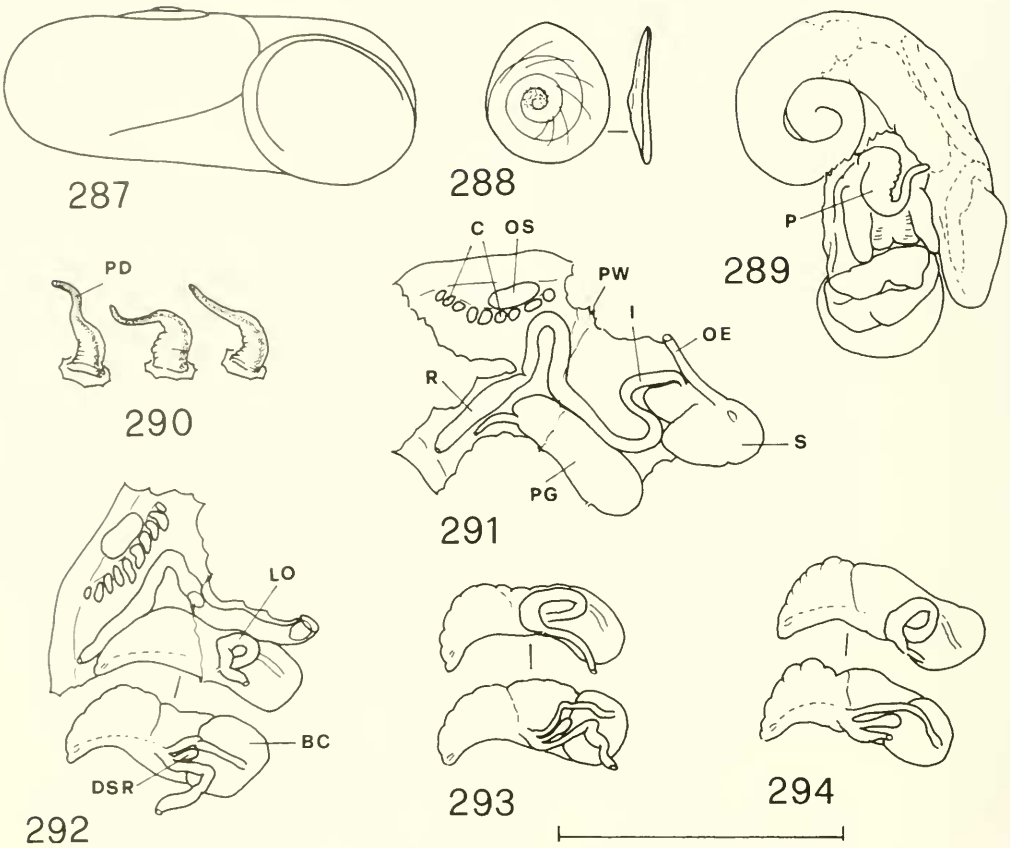
DESCRIPTION OF A NEW VALVATIFORM GENUS FROM FRANCE

Some of the species mentioned in the present paper and studied anatomically in the course of its preparation were found to belong to genera which have not yet been described. Here we only describe one, the type species of which was already known in the literature under an improper generic name.

***Heraultia* n. gen.**

Diagnosis

Hydrobiid snail with shell very small, planispiral, whitish, anatomically characterized by: male genitalia with penis conical, pointed, without lobes; female genitalia with distal seminal receptacle and a bursa copulatrix; bursa copulatrix very large, with very long



FIGS. 287–294. Shell, operculum and anatomical details of *Heraultia exilis* (Paladilhe, 1867) from the spring of the Lez River, Hérault, France, M. Bodon leg. 2.12.84. Fig. 287: shell; Fig. 288: outer face (left) and profile (right) of operculum; Fig. 289: body of a male with pallial cavity open to show head and penis; Fig. 290: dorsal side of penis of three males; Fig. 291: prostate gland, stomach, intestine and pallial organs of a male; Fig. 292: renal and pallial oviduct, intestine and pallial organs of a female; Figs. 293–294: renal and pallial oviduct of two females. Scale bar = 1 mm.

duct entering bursa on lateroposterior side; central tooth of radula with one basal cusp on each side.

Etymology

From Hérault, the Department of France, in which the species occurs.

Type Species

Valvata exilis Paladilhe, 1867.

Taxonomy

See discussion of *H. exilis.*

***Heraultia exilis* (Paladilhe, 1867)**

Valvata exilis Paladilhe, 1867: 51–52, pl. 21, figs. 27–30.

Type Locality: ". . . dans les fossés d'irrigation des prairies de la rive droit du Lez à la hauter du hameau de Lattes . . . Elle se rencontre aussi en petit quantité dans les alluvions du Lez recueillies sous le village de Castelnau, à près de 8 kilomètres en dessus de Lattes. Mais elle paraît bien plus abondante dans les alluvions de la Boyne (sous le village de Fontès, arrondissement de Béziers) . . .", Hérault, France.

Type Material: syntypes (shells) in the Pal-

adilhe collection, Faculté des Sciences, Montpellier, France (Boeters, 1974).

Material Examined

- Source du Lez, Hérault, France, M. Bodon leg. 2.12.1984 (3 males, 5 females, many shells), 4.9.1985 (many shells).
- Debris of the Lez River, Prades-le-Lez, Hérault, France, M. Bodon leg. 5.1.1992 (4 shells).
- Debris of the Lez River, Castelnau, Montpellier, Hérault, France, M. Bodon leg. 3.12.1984 (many shells).
- Debris of the Mosson River, Juvignac, Montpellier, Hérault, France, M. Bodon leg. 4.9.1985 (2 shells).

Description

Shell very small, planispiral, thin, pale whitish, waxen, transparent when fresh; surface of protoconch malleated; spire flat, consisting of 2.25–3 rapidly growing convex whorls; last whorl large, dilated, descending to some extent near aperture; umbilicus wide; aperture prosocline, roundish; peristome complete, slightly sinuous at upper margin, slightly thickened, reflected especially at lower and columellar margin (Figs. 213, 287; Paladilhe, 1967: 51, pl. 21, figs. 27–30; Locard, 1889: 329; 1893: 127; Germain, 1913: 323; 1931: 678; Boeters, 1974: fig. 8). Dimensions: height = 0.48–0.68 mm; diameter = 1.05–1.54 mm.

Operculum slightly thickened, yellowish, paucispiral, thicker at centre of inner face, but without peg (Fig. 288; Boeters, 1974: 86).

Body unpigmented; eye spots absent (Fig. 289; Boeters, 1974: 86).

Male genitalia with prostate gland bulging slightly into pallial cavity; penis rather long, conical, having short, wide basal portion with corrugated sides and longer, gradually tapering, apical portion ending in very pointed tip; penial duct zig-zagging through right portion of penis to open at penis tip (Fig. 290; Boeters, 1974: 83, fig. 3).

Female genitalia with distal seminal receptacle and a bursa copulatrix arising from distal renal oviduct; seminal receptacle, club-like, small but proportionally rather developed, arising from oviduct very close to point of origin of duct of bursa copulatrix; bursa copulatrix large, sac-like, oval to square in outline, with very long, slender duct entering bursa at lateroposterior side; seminal groove running along ventral side of capsule gland (Figs. 292–294; Boeters, 1974: 83, fig. 4). Bursa copulatrix incorrectly depicted by Boeters (1974: fig. 4) as rather small with duct entering on anterior side.

Radula with central tooth trapezoidal with long lateral wings and basal tongue, its apical margin V-like with long, robust central denticle and 4–5 smaller denticles on both sides, in decreasing order of size; one basal cusp where each lateral wing arises from face of central tooth; lateral teeth rake-like, apically enlarged, their anterior margin with 9–10 denticles, central one longer, larger; first marginal teeth rake-shaped, with long lateral wing and elongated cutting edge with long row of 23–25 small denticles anteriorly; second marginal teeth scraper-shaped, with long slender lateral wing and roundish, spoon-like apex, its cutting edge carrying rather long row of 18–20 small denticles (Figs. 177–179).

Stomach without posterior caecum; intestine with rather well-developed, U- or V-like bend on pallial wall (Figs. 291, 292; Boeters, 1974: 86, fig. 3).

Osphradium oval or kidney-shaped; ctenidium consisting of 9–12 lamellae (Figs. 291, 292; Boeters, 1974: 86).

Taxonomy

Boeters (1974) assigned *Valvata exilis* to *Horatia* Bourguignat, 1887, which, at that time, was known to be characterized by: rather large bursa copulatrix and distal seminal receptacle (c.f., Radoman, 1966; Radoman, 1973b). More recent anatomical study of *Horatia* revealed that the female genitalia not only have a bursa copulatrix and distal seminal receptacle, but also a proximal seminal receptacle (Fig. 108; Radoman, 1983). Clearly, *V. exilis* does not belong to *Horatia,* and our anatomical study of specimens collected near the type locality brought to light new data which supports the introduction of a new genus.

Only one of the genera with valvatiform shells described so far is close to *Heraultia,* that is, *Arganiella* Giusti & Pezzoli, 1980 (see above). *Arganiella* is characterized by a penis lacking lobes and by female genitalia with a large bursa copulatrix and only the distal seminal receptacle. Our decision to introduce *Heraultia* is prompted by the fact that *Arganiella* is clearly distinguished by: penis dilated subapically and with shorter apical portion; bursa

copulatrix having a rather short duct entering on the anterior side; central tooth of radula with two basal cusps on each side.

Heraultia exilis was reported from Spain by Alonso (1975), Vidal-Abarca & Suarez (1985) and Bech (1990). All these reports are based on shell material and are therefore unreliable.

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